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CONTENTS

PAGE

SALMON, J. T. Concerning the COLLEMBOLA ONYCHIURIDAE . . . . . 119–156, 84 figs.

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CONCERNING THE COLLEMBOLA ONYCHIURIDAE

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(*University of Wellington, New Zealand*)

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With 84 Text-figures

Contents

PAGE

Part I. The Classification of the Tullbergiinae and Onychiurinae
1. Introduction 119
2. Morphological features of a typical Collembolan . . 120
3. Taxonomic history of the genus *Onychiurus* Gervais and the status of the subfamilies of the Onychiuridae and their included genera 124
4. Key to the subfamilies and genera of the Onychiuridae . 129

Part II. The Onychiurinae Described by Bagnall, with a Review of the Onychiurid Material in the British Museum (Natural History)
1. The subfamily Tetrodontophorinae Stach, 1954 . . 131
2. The Onychiurinae described by R. S. Bagnall, with notes on some of Börner's type specimens 132

Part III. Two New Species of Onychiurinae 155

summary 156

PART I

The Classification of the Tullbergiinae and Onychiurinae

1. *Introduction*

While in England at the British Museum (Natural History)[1] during 1951, I was able, in addition to examining the types of Collembola in the collections, also to have access to the types and paratypes of some of Dr. R. S. Bagnall's species of Onychiuridae. Later I had the pleasure of meeting Dr. Bagnall and he kindly made available to me the remainder of his collection of Collembola which he still held. All his specimens were mounted on microscope slides, and in the intervening years I have been studying this material. It is unfortunate, to say the least, that I find it imperative to deal very critically with Bagnall's work on the Onychiuridae, much of which falls far short of modern taxonomic standards.

[1] During the tenure of a Nuffield Foundation Fellowship in England.

Quite soon I came to realise that, though Bagnall possibly had a flair for detecting new species, his descriptions, which in most cases were not accompanied by any illustrations, were hopelessly inadequate. In fact, sometimes they bear little resemblance to the actual specimens labelled as the type or the paratypes in his collection. All the preparations were very badly made, and most had to be remounted before a detailed and accurate study could be made.

From the condition of his material, the poorness of his descriptions, the all embracing nature of his *Contributions to a knowledge of the Onychiuridae* published in 1949 (*Ann. Mag. nat. Hist.* (12) 2 : 498–511), and in the light of the numerous criticisms of his genera and species made by Stach in that author's 1954 monograph (*The Apterygotan fauna of Poland in relation to the world fauna of this group of insects.* Family Onychiuridae, 219 pp. Cracow) it became painfully evident that a critical and thorough revision of all Bagnall's work on the Onychiuridae was essential. Accordingly in this paper I offer the first instalment of this revision.

This has proved an extremely long, difficult and involved task, largely on account of the very bad condition of many of his specimens. Finally, however, I have been able to decipher the essential morphological details for all the species represented in his collection. All the specimens have been examined several times under transmitted light and under two phase contrast systems of the microscope, one by Watson of London and the other by Zeiss of Oberkochen, West Germany. In all cases I am satisfied that the descriptions which I now give of Bagnall's species are correct, and that the figures I have prepared are accurate illustrations of the respective parts and details involved in each case. Stach accepted most of Bagnall's species, perhaps with some misgivings, in his 1954 work, and placed them in his key to the Onychiurinae, but, owing to the inadequate nature of the original descriptions, Bagnall's species which are valid all appear in Stach's key in wrong and unrelated positions. Consequently the user of Stach's key must ignore Bagnall's species included therein.

While at the British Museum (Natural History) I was also fortunate in being able to study other Onychiurid type material, including some from the Börner collection purchased from Carl Börner in 1908. Most of these species have never before been illustrated, so I am taking this opportunity to illustrate and discuss them also.

2. *Morphological features of a typical Collembolan*

Taxonomy should reflect the relationship of different forms to one another and their places in a natural scheme of classification, based preferably on evolutionary development and sequences. I therefore take a typical Onychiurid Collembolan and consider its morphological features from the standpoint of possible evolutionary development.

The Pseudocelli

These organs, probably developed as specialised sensory areas, should first appear as pits or depressions associated with a thinning of the cuticle above, or adjacent to, sensory structures of the lower epidermis. As such they would at first be without integumentary or chitinous borders and would

appear as seen in the genus *Kalaphorura* Abs. As evolutionary development proceeded, these simple pits could become chitinised with thick protective borders and " combs ", as seen in the pseudocelli of all true species of *Onychiurus*. It would seem to me, therefore, that the separation of *Kalaphorura* from *Onychiurus* by Absolon was sound and in accordance with present day trends in taxonomic research.

The pseudocelli of the Onychiurinae have been extensively used in the past by many authors as specific characters. Much reliance has been placed by some authors, and, indeed, myself, on the number of pseudocelli on each body tergite. I have noticed repeatedly, in working through Onychiurid material, that the number of pseudocelli on individual body tergites can vary, sometimes quite considerably, between specimens of the same species and even between the two sides of the same individual. The well-known *Protophorura armata* (Tullb.), for instance, may have to each side, 2, 3 or 4 pseudocelli on the posterior margin of the head, 1–3 on Th. II and Th. III or 2–4 on Abds. IV and V. *Onychiurus fimetarius* L. shows a similar type of variation in the number of dorsal pseudocelli ; these may vary between 2–3 on Th. III, 4–5 on Abd. IV and 2–4 on Abd. V. I have examined specimens of *fimetarius* with 3 pseudocelli on one side of Abd. V but only 2 on the other side. Similarly, specimens of *Protaphorura armata* are quite common with 3 pseudocelli on one side of the posterior margin of the head but 4 on the other side. Stach records that in *O. fimetarius* Th. I may have 1 + 1 pseudocelli or they may be entirely absent. Variations of this nature are recorded for *O. ambulans* (Nic.) and other species. All this leads me to express the opinion that small variations in the numbers of pseudocelli on the tergites are not of sufficient importance to serve, by themselves, as characters for the separation of species. On the other hand, large variations in the number, or the presence or absence of pseudocelli on a given tergite, probably are good specific characters. Except for those on the antennal base area and on the posterior margin of the head, differences between individuals of less than three in the number of pseudocelli on a given tergite should not I consider be used as characters for the separation of species. The pseudocelli of the antennal base area, the posterior margin of the head and Th. I, however, do appear to be reasonably constant in number for any given species ; their number and arrangement may be regarded as useful taxonomic characters.

The Sensory Organ of Ant. III

This structure could appear first as one or more simple, smooth sensory clubs, quite unprotected, as seen in the genera *Tullbergia* and *Paleotullbergia*. As evolution proceeded, these sensory clubs could become specialised by the development of particular shapes, or by the development either of surface structures such as granules, tubercles and papillae, or reticulations, foliations and lamellae. Furthermore, chitinous ridges could develop for the protection of the sense clubs, as in some genera of the Tullbergiinae, and conceivably such ridges could become subdivided, as seen in *Pachytullbergia* Bonet, to form the papillae which protect the sense clubs in the Onychiurinae. The occurrence of guard setae would be a natural secondary development. In this way it is possible to trace the complicated structures and combinations of structures seen in this organ throughout the various species of the Tullbergiinae and Onychiurinae.

The Postantennal Organ

This organ, which probably reaches its highest development in the Collembola amongst the species of Onychiurinae, is one which disappears in the more highly developed Collembola, and therefore it seems reasonable to regard it as indicative of primitive, or what might perhaps be better termed early, forms of Collembola. The simplest form in which the postantennal organ appears is a depression of elliptical or almost circular outline. This then produces vesicles which can be arranged in either of two ways—haphazardly in rows, or in a circular form around a rosette. This simple form is seen in the "*affinis*" group of *Onychiurus*. The vesicles arranged more or less haphazardly can be seen in the "*sibiricus*" group of *Onychiurus* and certain forms of Tullbergiinae, such as *Neotullbergia laingi* Bagnall. As evolution of the organ advanced, these vesicles became more regularly arranged, a tendency which is evident in some species belonging to the "*sibiricus*" group. In many species of the Tullbergiinae the simple vesicles become arranged in two more or less closely packed parallel rows lying at an angle with the long axis of the organ, as seen in *Tullbergia affinis* Börner and *Dinaphorura diversispina* Wom. Further development results in vesicles of specialised shapes, as seen in *Metaphorura borneri* Bagnall. The stage is then reached, illustrated by the "*armatus*" group of *Onychiurus*, in which there are a number of vesicles arranged at right angles to the long axis of the ellipse which forms the organ. Species such as *Stenaphorura denisi* Bagnall in the Tullbergiinae have also developed to this stage. Further evolution results in the division or budding of the vesicles to produce new tubercles, so that the vesicles of the postantennal organ, instead of being simple, become compound. This development can be traced through the species *Onychiurus tuberculatus* (Moniez) and *O. paxi* Stach, and results in the compound or tuberculated type of organ seen in what we call the "*ramosus*" or "*fimetarius*" groups. The end product is the compound tuberculated postantennal organ seen in *Onychiurus dentatus* (Folsom). It seems reasonable to utilise these evolutionary stages in the development of this organ in a scheme for the classification of the Onychiurinae.

The Furcula

This organ is a specialised development which appears in the more highly evolved Collembola, and is normally regarded as a characteristic feature of the Order. Rudiments of the furcula appear in certain species of the Onychiurinae, and it may be either that these rudimentary structures, referred to as furcal ridges and so on, mark the beginning of the development of the furcula or that, in this particular line in Collembola, the stimulus for the evolution of the furcula was not sufficiently strong to result in its complete development, so that the furcal ridges and rudiments are really vestiges of development that are tending to disappear. However, as the organ does appear fully developed in *Tetrodontophora*, it seems to me that these structures in *Onychiurus* are rudiments. They are, nevertheless, useful in the taxonomy of the group.

The Foot

The primitive insect foot consists of a claw and accessory claw or unguiculus, and there is a tendency for reduction or specialisation in structure of the ungui-

culus. This must therefore be a secondary evolutionary development, and a small reduced unguiculus in Collembola is vestigial.

Clothing

Scales are not present amongst the Onychiuridae, but scales are a specialised development from setae. In fact, the evolution of scales from setae can be seen on the body of single individual specimens amongst the Paronellinae. Primitive setae are undifferentiated—that is, they are neither ciliated nor serrated, so that the clothing of simple setae seen in the Onychiuridae is a primitive feature of this family, and is one of the primary reasons why I regard the Onychiurid Collembola as primitive in the sense that they represent an early development in the evolution of Collembola. The setae and scales of Collembola have been used by several workers as taxonomic characters. Börner and Schott both considered clothing structures of great value in deriving the basic classificatory divisions. More recently, Cassagnau and Yosii have used the chaetotaxy in Collembola as systematic characters. In a recent paper of my own dealing with the Paronelline Collembola, I have stressed the value of the microscopic structure of the scales in the systematics of this group. During my present study of the Onychiuridae I have repeatedly noticed that the arrangement of the setae in association with the anal spines on Abd. VI appears to be of considerable value taxonomically and accordingly in this paper I have included details of these structures wherever it has been possible to decipher them clearly.

Anal Spines

These structures, often referred to as " anal horns ", are normally present in all the Onychiuridae. In the Onychiurinae there are never more than two, which are always simple, their greatest diversification being the evolution of integumental papillae upon which the spines are mounted. In the Tullbergiinae, however, evolution of anal spines is highly developed ; in addition to those mounted posteriorly on Abd. VI, the " true " anal spines, there are frequently many additional dorsal spines, as seen in the genera *Stenaphorura* and *Dinaphorura*. In the genus *Neotullbergia* the anal spines have evolved further by the acquisition of ornamentation in the form of branches. These developments of the spination of Abd. VI provide useful taxonomic criteria which were applied by Bagnall in 1935 for the classification of his newly created subfamily Tullbergiinae.

From the point of view of systematics, large unwieldy genera are difficult to manage, but the arbitrary splitting of existing genera and the creation of new, strictly unrelated ones does not necessarily advance taxonomy. If, however, the creation of new genera can be related to evolutionary sequences, the fundamentals of taxonomy and the desires of the systematist can both be satisfied.

From the arguments given above, I think it is reasonable to attempt the splitting of the genus *Onychiurus*, as presented by Stach and others, into several related genera ; but before doing this I should like to survey briefly the taxonomic history of this genus.

3. *Taxonomic History of the Genus* Onychiurus *Gervais and the Status of the Subfamilies of the Onychiuridae and their included Genera*

The genus *Onychiurus* was established by Gervais in 1841, and later that year (*Echo monde savant* **8** : 372) he fixed the type as *O. ambulans* Degeer, 1779, so that all species of *Onychiurus* with smooth sense clubs in the sense organ of Ant. III, and a compound or tuberculated postantennal organ, must belong here. Since the time of Gervais both Folsom and Stach have placed all the *Onychiurus*-like Collembola together without any separation into subgenera or species groups, and other workers, notably Handschin and Gisin, have attempted to break down *Onychiurus* into several species groups based on the structure of the postantennal organ. In so doing they appeared to overlook the importance of the sensory organ on Ant. III, and the work done in this regard on the classification of *Onychiurus* by both Absolon and Börner in the early 1900's. Gisin, in 1944 (Materialien zur Revision der Collembolon, *Mitt. schweiz. ent. Ges.* **19** : 121–56), published keys for the separation of the species of *Onychiurus*, using the species group system. While working on the British Onychiuridae, Bagnall recognised that the genus *Onychiurus* split naturally into several closely related genera. In 1935 he divided the family Onychiuridae into the subfamilies Tullbergiinae and Onychiurinae on the basis of the structure of the sensory organ of Ant. III, and this division has met with general approval. Later, in 1948, he erected six new genera for certain forms of *Onychiurus* ; some of these genera appear to be valid, and a worthwhile contribution to the systematics of the group. However, in 1949 Bagnall created three new subfamilies of Onychiuridae, and split off from *Onychiurus s. str.* another 15 new genera on the basis of characters which are of no more than specific value. These are simply paper genera, culled from the literature without reference to or study of actual specimens. Furthermore, they have little taxonomic relationship to one another, nor do they show any evolutionary sequence. Stach, in his 1954 monograph on the Onychiuridae, refers to " Bagnall, who created a new genus for almost each species of Onychiuridae . . .".

In the scheme which I am proposing, however, several of Bagnall's genera are valid, and we must recognise that he did make valuable contributions towards the classification of the Onychiurine Collembola. The first real step in this direction was made by Absolon in 1901, when he set up the genera *Protaphorura* and *Deuteraphorura*, basing his distinctions on the form of the postantennal organ. In 1909 Börner went further, introducing the structure of the sensory organ on Ant. III as a character in the classification of the genus. This amounts to the further application to the genus *Onychiurus* of the character which had been used to separate it from the genus *Tullbergia*. According to Börner, those forms with smooth sense clubs constitute the genus *Onychiurus* Gervais, and those with granulated or tuberculated sense clubs form the genus *Protaphorura* Absolon, with *Protaphorura* (*Onychiurus*) *armata* (Tullb.) as the type species (1909, *S.B. Ges. naturf. Fr. Berl.* **2** : 102). At the same time, Börner designated *O. inermis* Tullb. as the type species for the genus *Onychiurus*, but in doing this he was in error, for Gervais had already in 1841 so designated *O. ambulans* L. Bagnall was really following the ideas of Absolon and Börner to their logical conclusion when he proposed several new genera for the reception of those forms of *Onychiurus* normally classified in the " *ramosus* " and " *sibiricus* " groups, etc.

With reference now to Bagnall's 1949 paper, the subfamily Psyllaphorurinae, through its single genus *Psyllaphorura*, represents only an advanced stage in evolution of the post antennal organ, and an early stage in the development of the pseudocelli and the sensory clubs of the sense organ on Ant. III. It otherwise resembles *Onychiurus*. The genus, however, is a good one, but the subfamily Psyllaphorurinae is a synonym of the subfamily Onychiurinae.

Bagnall's suggestion that the pseudocelli inside the antennal base area are distinct from the usually single pseudocellus outside it, and his use of this character for supra-specific classification has no justification, particularly as the area is frequently not marked by any cuticular differentiation.

The Subfamily Oligaphorurinae

This subfamily was discussed by Stach (1954 : 71), in whose opinion all four of the genera included are superfluous because the differences given by Bagnall are merely of specific importance. With this opinion I entirely agree. Stach, however, does suggest that the subfamily name Oligaphorurinae might be accepted into systematics for the "*affinis*" group of *Onychiurus* in which the postantennal organ consists of 3–4 vesicles only. I can see no reason at all for diagnosing a new subfamily here. I do, however, consider that a new generic name within the family Onychiurinae can be introduced for those species of *Onychiurus* in which the postantennal organ is in the simplest form of not more than four vesicles arranged as a rosette. I propose, therefore, that Bagnall's genus *Archaphorura*, type species *O. serratotuberculatus* Stach, 1933, be accepted for those forms previously regarded as belonging to the "*affinis*" group. The subfamily Oligaphorurinae is synonymous with the subfamily Onychiurinae, and the genera *Oligaphorura* and *Micraphorura* are both synonyms of *Archaphorura* as defined in this paper, the differences cited by Bagnall being only of specific rank.

The genus *Dimorphaphorura*, distinguished by Bagnall on the character of coarse granulations on Abd. VI, cannot be upheld, and becomes a synonym of *Archaphorura* Bagnall as defined in this paper. The name *Archaphorura* takes page priority over *Dimorphaphorura*.

The Subfamily Protaphorurinae

Bagnall erected this subfamily primarily to include those species previously regarded as belonging to the "*armatus*" group or the genus *Protaphorura*. Its erection on such slender specific differences is an unwarranted extravagance in systematics ; it is quite untenable, and is synonymous with the subfamily Onychiurinae.

Of the eleven genera Bagnall included within this subfamily, seven of which were described as new, *Protaphorura* Abs., *Kalaphorura* Abs., *Spelaphorura* Bagnall and *Hymenaphorura* Bagnall are valid. Of the other genera, *Thalassaphorura* Bagnall is a synonym of *Spelaphorura* Bagnall as now defined in this paper. *Allaphorura* is a synonym of *Protaphorura*. The erection of a new genus on the basis of a slight widening or narrowing of the elliptical form of the postantennal organ and the presence or absence of anal spines, is quite unwarranted, as both these sets of characters are of specific importance only and not of family rank. The genus *Stenonychiurus* is also a synonym of *Prota-*

phorura. The differences cited in the structure of the postantennal organ are only of specific rank, and could in fact be artificial effects arising from shrinkage in mounting. The genus *Heteronychiurus* is also a synonym of *Protaphorura*. The fact that the two sense clubs of the sensory organ on Ant. III are of different shapes and granulation is a specific character only and not of generic rank. The genus *Hymenaphorurodes* is a synonym of *Hymenaphorura* Bagnall, as defined in this paper. The generic differences in the postantennal organ cited by Bagnall are the normal differences found in the examination of species belonging to *Hymenaphorura*. The genus *Protaphorurodes* I consider, from an examination of Yosii's figures and description of *T. tomuraushensis*, which Bagnall cites as the type species for this genus, a synonym of *Protaphorura* Abs.

The Subfamily Onychiurinae

In his 1949 paper Bagnall also erected three new genera in this subfamily. Of these, *Onychiuroides* becomes a synonym of *Paronychiurus* Bagnall as defined in this paper. Bagnall appears to have been very haphazard in the use of this name, for he published the species *O. michelbacheri* in 1948 without any generic diagnosis, and in 1949, in connection with the species *O. spinosus*, he says *Onychiuroides* is " for *edinensis* Bagnall and others ", implying that the species *O. edinensis* was the one he had in mind as the type species ; in his paper in the *Annals and Magazine of Natural History* issued in June 1949 (Series 12, Vol. 2), *Onychiuroides* is defined and the type given as *O. postumicus* Bonet. Whichever species is regarded as the type, this genus becomes a synonym of *Paronychiurus*, and as *Paronychiurus* appeared first in the literature it takes priority over *Onychiuroides*.

The genus *Neonychiurus*, by virtue of the type species *O. millsi* Chamberlain, is synonymous with *Pseudonychiurus* Bagnall as defined in this paper. The name *Pseudonychiurus* takes priority through earlier publication.

The genus *Argonychiurus*, by virtue of the type species selected, is a synonym of *Paronychiurus* as defined in this paper. The " tenent hairs " mentioned by Bagnall as a generic character are seen in other species of Onychiurinae, and are only of specific rank.

The genus *Micronychiurus :* although the post antennal organ of the type specimen of *O. minutus* Denis is slightly unusual in appearance, it would seem to me to represent the evolutionary development of the compound tuberculated postantennal organ of *O. ambulans* (Nic.) towards that of *O. dentata* Tullb. In *minutus*, however, the vesicles are still clearly visible as distinct units, and the species is a true *Onychiurus*. The genus *Micronychiurus* then becomes a synonym of *Onychiurus*.

Stach, in his 1954 monograph, proposes four new subfamilies to contain the somewhat aberrant genera hitherto included in one or other of the two subfamilies, Tullbergiinae or Onychiurinae. Of these the genus *Pachytullbergia* Bonet, 1947, represents to me a very simple form of Onychiurinae in which the post antennal organ is " *sibiricus* "-like and the sense organ of Ant. III has a protective skin fold which is subdivided into very broad plate-like papillae indicative of an early stage in the evolution of this organ. In general body outline the species *P. scabra* is rather *Neanura*-like, but its sensory structures are *Onychiurus*-like. I consider that the large number of rather specialised

shapes of some of the sense clubs in the sensory organ of Ant. III, the unusual body shape, the presence of tenent hairs and the absence of pseudocelli, taken together are of sufficient importance to justify the erection of Stach's new subfamily Pachytullbergiinae.

The genus *Paleotullbergia* Del. Deb., 1951, appears from the literature to be a simple form of Tullbergiinae, but I can find no group of characters of sufficient importance either singly or taken together to justify the creation of the new subfamily Paleotullbergiinae. The absence of pseudocelli places this subfamily with the Pachytullbergiinae in evolutionary sequence, and I think that taxonomically the two subfamilies, as suggested by Stach, are almost identical. The sensory organ on Ant. III of *Paleotullbergia* is also very simple and indicative of an early stage in its evolution, though more *Tullbergia*-like than *Onychiurus*-like ; it does not serve as a taxonomic character of subfamily rank. Accordingly I intend to regard the subfamily Paleotullbergiinae as a synonym of Pachytullbergiinae.

The new subfamily Tetrodontophorinae is, I think, justified on evolutionary grounds by the complicated nature of the sense organ of Ant. III, and the presence of a well developed furcula in all genera and species belonging here. I do not consider, however, that the subfamily Lophognathellinae is justified on any such grounds, and believe it taxonomically incorrect to separate this subfamily from the Onychiurinae.

If the evolutionary tendencies mentioned above are used, a scheme of generic classification can be devised for the subfamily Onychiurinae, in which *Onychiurus* is split into the following genera :

(a) *Kalaphorura* Absolon, 1901. Pseudocelli without chitinised borders ; postantennal organ of simple vesicles lying at right angles to the main axis of the organ ; sense clubs in sense organ of Ant. III either smooth or granular. Type species, *Kalophorura* (*Lipura*) *tuberculata* Moniez, 1891, as fixed by Börner, 1909 (*S.B. Ges. naturf. Fr. Berl.* **2** : 102).

(b) *Arcaphorura* Bagnall, 1949. Pseudocelli with chitinised borders ; postantennal organ of simple vesicles arranged as a rosette ; sensory organ of Ant. III with smooth or only faintly granulated sense clubs or the sense clubs granulated in part only. Type species, *Arcaphorura* (*Onychiurus*) *serratotuberculatus* Stach, 1933.

(c) *Absolonia* Börner, 1901. Pseudocelli with chitinised borders ; postantennal organ of tuberculated vesicles arranged as two parallel rows at right angles to the long axis of the organ ; sensory organ on Ant. III with granulated sense clubs and serrated or granulated *sense rods*. Type species, *Absolonia* (*Aphorura*) *gigantea* (Absolon), 1901.

(d) *Onychiurus* Gervais, 1841. Pseudocelli with chitinised borders; postantennal organ elongate oval, composed of vesicles subdivided into many tubercles, the vesicles lying at right angles to the long axis of the organ ; sense clubs of sensory organ of Ant. III smooth. Type species, *O. ambulans* L.

(e) *Hymenaphorura* Bagnall, 1948. Pseudocelli with chitinised borders ; postantennal organ elongate with simple vesicles lying more or less parallel to the axis of the organ ; sense clubs of sense organ of Ant. III granulated. Type species, *Hymenaphorura* (*Lipura*) *sibirica* (Tullb.), 1876.

(f) *Protaphorura* Absolon, 1901. Pseudocelli with chitinised borders; postantennal organ elongate oval with simple vesicles arranged at right angles to the long axis of the organ ; sense clubs of sensory organ of Ant. III granulated. Type species, *Protaphorura* (*Onychiurus*) *armata* (Tullb.), 1869.

(g) *Spelaphorura* Bagnall, 1948. Pseudocelli with chitinised borders; postantennal organ elongate oval with simple vesicles arranged at right angles to the long axis of the organ; sense clubs of sensory organ of Ant. III reticulate, foliated, laminated or with projecting lamellae. Type species, *S. glennei* Bagnall, 1948.

(h) *Paronychiurus* Bagnall, 1948. Pseudocelli with chitinised borders; postantennal organ elongate oval, with compound or tuberculated vesicles at right angles to the long axis of the organ; sense clubs of sensory organ of Ant. III granulated. Type species, *Paronychiurus* (*Onychiurus*) *ramosus* (Folsom), 1917.

(i) *Pseudonychiurus* Bagnall, 1948. Pseudocelli with chitinised borders; postantennal organ elongate oval, consisting of a mass of tubercles in which differentiation into vesicles cannot be detected; sense clubs of sensory organ of Ant. III coarsely granulated or papillate. Type species, *Pseudonychiurus* (*Aphorura*) *dentata* (Folsom), 1902.

(j) *Psyllaphorura* Bagnall, 1948. Pseudocelli with chitinised borders; postantennal organ elongate oval, formed of compound mass of tubercles in which individual vesicles cannot be detected; sense clubs of sensory organ of Ant. III smooth. Type species, *Psyllaphorura* (*Onychiurus*) *obesus* (Mills), 1934.

(k) *Handschiniella* Bagnall, 1949. Pseudocelli with chitinous borders; postantennal organ elongate and broadly oval, of simple vesicles at right angles to long axis of organ; sense clubs of sensory organ of Ant. III smooth. Type species, *Handschiniella* (*Onychiurus*) *schokkei* Hand., 1919.

(l) **Metonychiurus** gen. n. Pseudocelli with chitinised borders, postantennal organ entirely absent; sense clubs of sensory organ on Ant. III granulated. Type species, *Metonychiurus* (*Onychiuroides*) *michelbacheri* (Bagnall), 1948.

The species *Metonychiurus michelbacheri* probably represents a highly evolved Onychiurine form in which the post antennal organ has been lost, and I feel somewhat reluctantly that a new monotypic genus should be erected to receive it. The synonymy of Bagnall's original generic name *Onychiuroides* has already been discussed, and as he chose the wrong type species for this genus I have now to propose the new name *Metonychiurus* to receive this unique species. If Bagnall had chosen his *michelbacheri* as the type species of his genus *Onychiuroides*, this, of course, would not have been necessary.

Bagnall appears to have been more conservative in his work on the Tullbergiinae than when dealing with the Onychiurinae, and I find that, with the exception of *Protullbergia*, all his genera in this subfamily are valid, though a number of his species are synonyms of previously well-known forms. These cases of synonymy do not, fortunately, affect any of the type species.

According to Bagnall, the genus *Protullbergia* differed from *Tullbergia* Lubbock in the number of pseudocelli on some of the body segments, and in the full development of the unguiculus. I have already pointed out in this paper that differences in the numbers of pseudocelli on any given body segments are not of generic significance. The full development of the unguiculus, cited by Bagnall, is likewise of insufficient importance to form a good generic character. The genus *Protullbergia*, therefore, in my opinion falls as a synonym of *Tullbergia* Lubbock.

At this stage it seems advantageous to set out my findings in a concise form, and I therefore give the following new and revised key to the subfamilies and genera of the family Onychiuridae in which these cases of synonymy are clearly indicated.

4. *Key to the Subfamilies and Genera of the Onychiuridae*

1 Pseudocelli present 3
– Pseudocelli absent . . . . . Pachytullbergiinae Stach, 1954 (= Paleotullbergiinae Stach, 1954) 2

2 Postantennal organ present; sensory organ on Ant. III with several both plain and lamellated sense clubs and 5 large papillae; feet with clavate tenent hairs; Abds. I–V with wart-like processes **Pachytullbergia** Bonet, 1947
– Postantennal organ absent; sensory organ on Ant. III with only 2 simple sense clubs and one papilla; clavate tenent hairs absent; abdominal tergites normal without wart-like processes **Paleotullbergia** Delamare-Debouteville, 1951

3 Body pigment generally present; furcula always present and well developed . . . . . Tetrodontophorinae Stach, 1954 4
– Body pigment generally absent, species usually white in colour; furcula either entirely absent or present in a reduced and rudimentary form only 5

4 Sensory organ on Ant. III with more than 5 granulated papillae, arranged in 2–3 transverse rows, and with 2 very coarsely papillated sense clubs; the maxilla head with toothed median shaft and serrated lamellae . . . . . **Tetrodontophora** Reuter, 1882 (= *Homaloproctus* Börner, 1909)
– Sensory organ on Ant. III never with more than 5 granulated papillae, always arranged in one row, and 2 granulated sense clubs; the maxilla head without median shaft and lamellae **Lophognathella** Börner, 1908

5 Sensory organ on Ant. III with the two sense clubs bent towards each other and usually provided with an accessory lateral club; without guard papillae; unguiculus present but generally in a reduced form only, with or without terminal bristles Tullbergiinae Bagnall, 1935 6
– Sensory organ on Ant. III with the two sense clubs either straight, or curved, with both clubs bent in the same direction, without lateral accessory club: guard papillae present and well developed; unguiculus present, usually well developed, with terminal bristle Onychiurinae Bagnall, 1935 (= Oligaphorurinae Bagnall, 1949, = Psyllaphorurinae Bagnall, 1949, = Protaphorurinae Bagnall, 1949) 15

6 Sensory organ on Ant. III with the sense clubs entirely exposed, without protecting cuticular fold; antennal base area generally present and demarcated by smaller cuticular granules **Tullbergia** Lubbock, 1876 (= *Boerneria* Willem, 1902, *Protullbergia* Bagnall, 1947)
– Sensory organ on Ant. III with the sense clubs protected by a cuticular fold or pocket; antennal base area generally absent 7

7 Sensory organ on Ant. III with sense clubs or sense rods or both . . 8
– Sensory organ on Ant. III without sense rods but with 2 large sense clubs each in a separate but adjacent cuticular pocket, and bent towards each other; Ant. IV without apical sensory knob **Paratullbergia** Womersley, 1930

8 Sensory organ on Ant. III with 2 inferior bent sense clubs, 2 superior bent sense clubs and 2 large outer sense rods; claw with 2 groups of clavate tenent hairs; unguiculus absent **Clavaphorura** Salmon, 1943

– Sensory organ on Ant. III with fewer sensory clubs and rods ; without clavate tenent hairs ; unguiculus present or absent 9

9 Abd. VI with at least 7 spines ; pseudocelli almond-shaped
Dinaphorura Bagnall, 1935

– Abd. VI with less than 7 spines ; the pseudocelli normal round-shaped 10

10 Sensory organ on Ant. III with 2 superior strongly curved sense rods, bent towards each other and sometimes an accessory lateral rod, 2 inferior sense rods, either straight or curved, the whole all more or less protected by a cuticular fold ; Ant. IV with an apical sensory knob 11

— Sensory organ on Ant. III with only one bladder-shaped sensory rod, transversely directed ; Ant. IV without apical sensory knob ; Abd. VI with 3–5 small rudimentary spines
Austraphorura Bagnall, 1947

11 Abd. VI with 2 *branched spines* . . . . **Neotullbergia** Bagnall, 1935

— Abd. VI with *simple* spines 12

12 Postantennal organ elongate elliptical with complex bifurcate vesicles lying at an acute angle with the axis of the organ ; Abd. VI with medioventral process and 2 large anal spines on papillae
Metaphorura Bagnall, 1936

— Postantennal organ otherwise ; Abd. VI without medioventral process 13

13 Postantennal organ with triangular unilocular vesicles ; Abd. VI with 4 anal spines and 2 spine-like papillae
Neonaphorura Bagnall, 1935

— Postantennal organ with elongate or fusiform vesicles, never triangulate 14

14 Abd. VI with 2 simple anal spines . . . **Mesaphorura** Börner, 1900

— Abd. VI with 4 simple anal spines . . . **Stenaphorura** Absolon, 1900

15 Pseudocelli with distinct chitinous borders 16

— Pseudocelli without distinct chitinous borders ; cuticle coarsely granulate ; rudiments of furcula generally present
Kalaphorura Absolon, 1901

16 Postantennal organ present and composed of either simple or compound tuberculated vesicles 17

— Postantennal organ absent ; sense clubs of sensory organ on Ant. III granulated . . . . . **Metonychiurus** gen. n.

17 Postantennal organ composed of simple vesicles arranged in a rosette, or in more or less parallel rows 18

— Postantennal organ composed of vesicles more or less completely covered by a secondary growth of small tubercles 22

18 Postantennal organ with not more than 4 5 vesicles arranged as a rosette ; sensory organ on Ant. III with smooth or granulated sense clubs . . . . . **Arcaphorura** Bagnall, 1949
(= *Oligaphorura* Bagnall, 1949, = *Micraphorura* Bagnall, 1949, = *Dimorphaphorura* Bagnall, 1949)

— Postantennal organ elongate or elliptical with the vesicles arranged in rows 19

19 The vesicles of the postantennal organ lying more or less parallel with the long axis of the organ or making an acute angle with it ; sensory clubs of sensory organ on Ant. III granulated
Hymenaphorura Bagnall, 1948
(= *Hymenaphorurodes* Bagnall, 1949)

— The vesicles of the postantennal organ lying at right angles with the long axis of the organ 20
20 The sense clubs of sensory organ on Ant. III smooth, undifferentiated
Handschiniella Bagnall, 1949
— The sense clubs of sensory organ on Ant. III not smooth 21
21 The sense clubs of sensory organ on Ant. III granulated
Protaphorura Absolon, 1901
(= *Allaphorura* Bagnall, 1949, = *Stenonychiurus* Bagnall, 1949, = *Heteronychiurus* Bagnall, 1949, = *Protaphorurodes* Bagnall, 1949)
— The sense clubs of sensory organ on Ant. III either reticulated, foliated, laminated or with projecting lamella-like processes
Spelaphorura Bagnall, 1948
(= *Thalassaphorura* Bagnall, 1949)
22 The vesicles of the postantennal organ, though tuberculated, still clearly visible as separate structures 23
— The vesicles of the postantennal organ no longer clearly visible as such; instead the postantennal organ appears as a mass of small tubercles 25
23 The sense clubs of sensory organ on Ant. III smooth, undifferentiated
Onychiurus Gervais, 1841
(= *Lipura* Burmeister, 1838, = *Anurophorus* Nicolet, 1841, = *Adicranus* Bourlet, 1843, = *Augenius* Gistel, 1848, = *Aphorura* MacGillivray, 1893, = *Deuteraphorura* Absolon, 1901, = *Euaphorura* Börner, 1901, = *Micronychiurus* Bagnall, 1949)
— The sense clubs of sensory organ on Ant. III differentiated, usually granulated 24
24 The *sense rods* in the sensory organ on Ant. III smooth
Paronychiurus Bagnall, 1948
(= *Onychiuroides* Bagnall, 1949, = *Argonychiurus* Bagnall, 1949)
— The *sense rods* in the sensory organ on Ant. III serrated or granulated
Absolonia Börner, 1901
25 The sense clubs of sensory organ on Ant. III smooth, undifferentiated
Psyllaphorura Bagnall, 1949
— The sense clubs of sensory organ on Ant. III coarsely granulated or papillated . . . . . **Pseudonychiurus** Bagnall, 1948
(= *Neonychiurus* Bagnall, 1949)

PART II

THE SPECIES OF ONYCHIURINAE DESCRIBED BY BAGNALL, WITH A REVIEW OF THE ONYCHIURID MATERIAL IN THE BRITISH MUSEUM (NATURAL HISTORY)

1. *The Subfamily Tetrodontophorinae Stach*, 1954

Tetrodontophora bielanensis Waga (Figs. 7–10)

1842, *Ann. Soc. ent. Fr.* **11** : 264.

This species is illustrated by Stach in his 1954 paper but his figure of the sensory organ on Ant. III does not show the papillated sense clubs, which are clearly visible in the specimen which I have figured, and which is part of the Carl Börner Collection now in the British Museum (Natural History). In other respects our figures agree very closely. At the time I made these drawings Stach's work had not appeared, and I felt that a specimen identified by Börner was well worth figuring for future reference.

Homaloproctus sauteri Börner (Figs. 1–6)

S.B. Ges. naturf. Fr. Berl. **1909** : 105.

This species has never been figured, and the drawings I have made are from a cotype in the Carl Börner Collection in the British Museum (Natural History).

2. *The Onychiurinae described by R. S. Bagnall, with Notes on some of Börner's Type Specimens*

Protaphorura armata (Tullberg) (Fig. 11)

Lipura armata Tullberg, 1869, *Akad. Afhandl. Uppsala* : 1–20.
Lipura incerta Moniez, 1893, *Rev. Biol. Nord France* **6** : 81.
Lipura ambulans Meinert, 1896, *Vidensk. Med. naturh. Foren. Kjobenhavn* **1896** : 154.
Aphorura armata Schaeffer, 1896, *Mitt. nat. Hist. Mus. Hamburg* **13** : 149.
Onychiurus armatus Börner, 1902, *Zool. Anz.* **24** : 696.
Aphorura ambulans Guthrie, 1903, *Rep. Geol. nat. Hist. Surv. Minnesota, Zool. Serv.* (**4**) : 1–110.
Onychiurus makarensis Salmon, 1937, *Trans. Roy. Soc. N.Z.* **67** : 352.

To the above primary synonyms of *P. armata* which, have been generally recognised, I can now add the following synonyms from Bagnall :

Onychiurus flavescens Bagnall, 1935, *Scot. Nat.* **1935** : 115, **syn. nov.**
Onychiurus flavidulus Bagnall, 1939, *Ent. mon. Mag.* **75** : 94, **syn. nov.**
Onychiurus daviesi Bagnall, 1935, *Scot. Nat.* **1935** : 113, **syn. nov.**
Onychiurus waterstoni Bagnall, 1937, *Scot. Nat.* **1937** : 145, **syn. nov.**

Three other slides in his collection labelled as types, one bearing the name *O. tenuispinus*, another *O. andrei* and the third *O. longisetosus*, I cannot trace in the published literature, but all three are further specimens of *P. armata*.

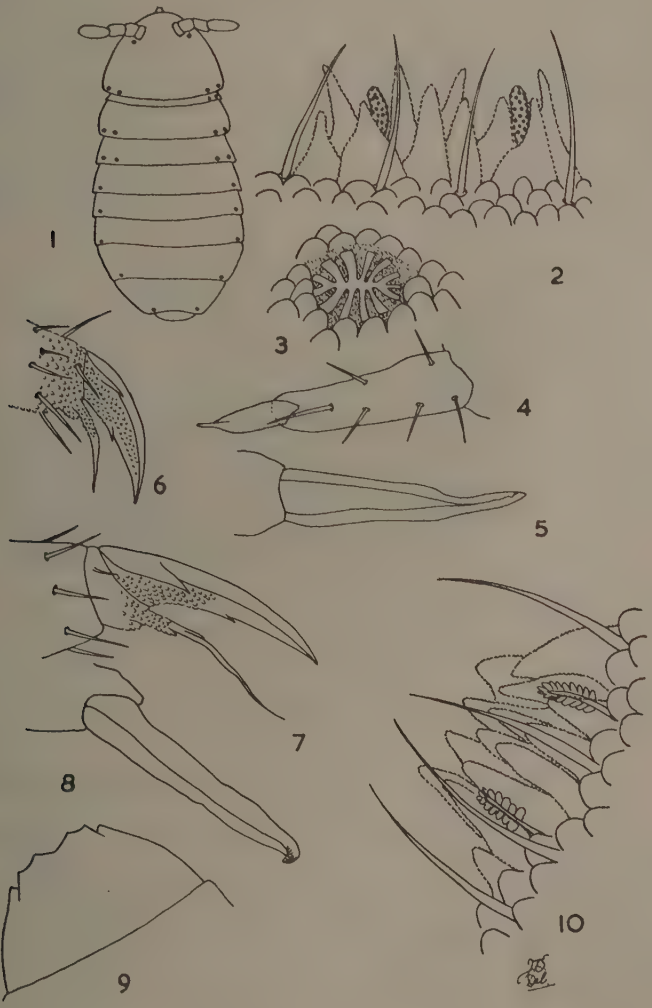
The following notes are added concerning these species described by Bagnall:

O. flavidulus nom. nov., 1939, for *O. flavescens* Bag., 1935 : I examined the type, three paratypes and two other specimens identified by Bagnall as *flavescens*. The vesicles of the postantennal organ varied between 32–36 and were of typical *armata* form ; the sensory organ on Ant. III was also of typical *armata* form ; the pseudocelli mentioned by Bagnall as occurring on Th. I could not be found on any specimen, and otherwise in both position and number they were as found in *armata*.

For *O. daviesi* I examined the type specimen and two others identified by Bagnall as *daviesi*. These specimens do not have particularly long and slender claws, but claws quite typical of *P. armata*. The anal spines similarly are typical of *armata*, measuring, on the type : spine 28, papilla 7, hind claw 56 ; and on one of the other specimens : 29, 5, 50 respectively. In all respects Bagnall's specimens are typical *P. armata*.

For *O. waterstoni* I have examined the type and two paratypes. The vesicles of the postantennal organ number up to 27 of typical *armata* form. The hind claws are not twice as long as the anal spines, as stated by Bagnall, but measure on the type specimen : spines 11, papilla 3, claw 21, with the adjacent long setae 25. The pseudocelli are as follows : Ant. base : 3 + 3 ; hind margin of head : 4 + 4 ; Th. I : 0 + 0 ; Th. II : 2 + 2 ; Th. III : 3 + 3 ; Abd. I : 2 + 2 ; Abds. II–III : 3 + 3 ; Abd. IV : 4 + 4 ; Abd. V : 3 + 3 ; which, though not typically *armata*, do not differ sufficiently to warrant the creation of a new species.

The posterior setae on Abd. VI of Bagnall's type specimen (fig. 11) agree absolutely in arrangement with those on typical specimens of *P. armata* I have examined. This, with the fact that *waterstoni* agrees with *armata* in all other respects except in minor differences in the pseudocelli, leads me to synonymize Bagnall's species with *P. armata*.



Figs. 1–10.—(1–6)—*Homaloproctus sauteri* Börner, drawn from cotype: (1) whole insect showing pseudocelli; (2) sensory organ on Ant. III; (3) pseudocellus; (4) mucrodens; (5) dens; (6) hind foot. (7–10)—*Tetrodontophora bielanensis* Waga, drawn from a specimen in the Börner Collection: (7) middle foot; (8) dens; (9) outline of Abd. VI; (10) sensory organ on Ant. III.

Protaphorura armata denticulata (Handschin) (Fig. 12) **comb. nov.**

Onychiurus armatus var. *denticulatus* Handschin, 1924, *Denkschr. schweiz. naturf. Ges.* **60** : 104.
Onychiurus subaequalis Bagnall, 1937, *Scot. Nat.* **1937** : 88, **syn. nov.**

Two further slides, one of which is labelled as a type, the other as a paratype of *O. aequalis* Bagnall, were present in Bagnall's collection. However, I can find no trace of any species under this name in the published literature but the two slides are also specimens of *P. armata denticulata* Hand.

With regard to *O. subaequalis*, I have examined the type specimen, which is not in good condition. It has a postantennal organ of the *armatus* type with 27 vesicles, and the sensory organ on Ant. III is of typical *armatus* form ; the pseudocelli are : Ant. base : 3 + 3 ; hind margin : 2 + 2 ; Th. I : 0 + 0 ; Th. II : 1 + 1 ; Th. III : 2 + 2 ; Abds. I–IV : 3 + 3 ; Abd. V : 2 + 2 ; anal spines 17, papillae 2, hind claw 15. The claw is typical of *denticulata* Hand., with a strong inner tooth near the centre.

Although there is some variation from the normal *armatus* form in the pseudocelli and anal spines, this is within the limits recognised for this species and its subspecies. The general appearance of this single type specimen suggests that it is an *immature* form of *P. armata denticulata.*

In his original description Handschin says this form is recognised by the greater number of papillae in the sensory organ on Ant. III, and by differences in the number of pseudocelli. Stach (1924, *Ann. Mus. zool. polon.* **10** : 132) discusses it and figures the claw, showing the clear inner tooth. In Bagnall's specimens the sensory organs on Ant. III all have the normal five papillae and five guard setae, and I can find no trace of the additional papillae mentioned by Handschin. Folsom (1917, *Proc. U.S. nat. Mus.* **53** : 645) mentions varieties of *P. armata* having six papillae instead of five in this sense organ, illustrating it in his figure 45.

While in Scotland in 1951 I collected, in several localities, specimens of an Onychiurid Collembolan which have proved to be this subspecies *denticulatus.* They were nearly always large, and pale yellow or pale lime-green in colour when alive.

The following brief description of this subspecies may be helpful to future students of the Collembola :

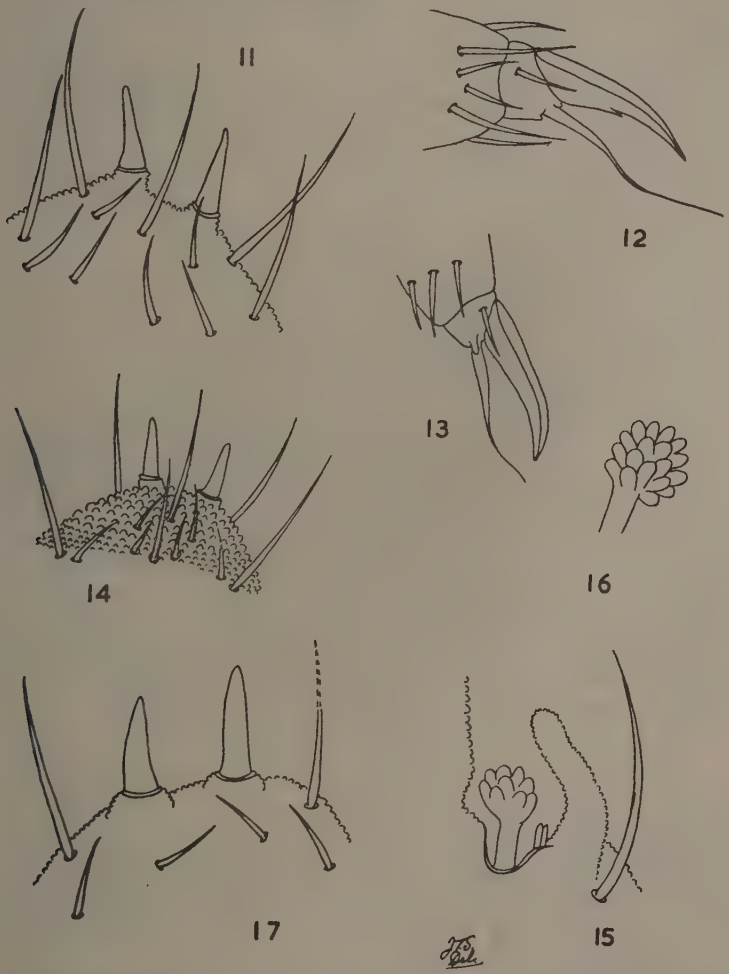
Colour : white, pale lime green or pale yellow when alive, fading rapidly in spirit to white.

Clothing : moderately well clothed with short plain setae, with longer setae both dorsally and posteriorly.

Body : length up to 2·25 mm. ; sensory organ on Ant. III of typical *P. armata* form but sometimes with the number of papillae increased to 6 ; antennal base area clearly marked by finer cuticular granules ; postantennal organ with 14–26 vesicles of typical *P. armata* form ; not 14–18 vesicles as described by Bagnall. Pseudocelli as follows :

Ant. base : 3 + 3 or 2 + 2 or 2 + 3.
Hind margin : 2 + 2 or 3 + 3.
Th. I : 0 + 0.
Th. II : 1 + 1, laterally placed.
Th. III : 2 + 2, widely separated.
Abd. I : 2 + 2, diagonally arranged, fairly close together.
Abd. II : 2 + 2 or 3 + 3, widely spaced in line across each side.

Abd. III: 2 + 2, widely spaced laterally.
Abd. IV: 3 + 3, 2 close together medially, one lateral to each side.
Abd. V: 3 + 3 closely spaced diagonally on each side.
Furcal ridge present; 2 anal spines on very small papillae or without papillae.
Foot: with single strong inner tooth at about, or just above, centre; unguiculus tapering with long whip-like flagellum which, if unbroken, always extends beyond apex of claw; claw with long basal seta to each side.



Figs. 11–17.—(11)—*Protaphorura armata* (Tullb.), Abd. VI showing anal spines and associated dorsal setae. (12)—*Protaphorura armata denticulata* (Handschin), hind foot. (13–16)—*Protaphorura caledonica* (Bagnall), drawn from type and paratypes: (13) hind foot from type; (14) apex of Abd. VI, reconstructed from type and a paratype; (15) side sectional view of sensory organ on Ant. III from a paratype; (16) sense club from sensory organ on Ant. III; (17)—*P. stachi* (Bagnall), anal spines and associated dorsal setae.

Protaphorura caledonica (Bagnall) (Figs. 13–16) **comb. nov.**

Onychiurus caledonicus Bagnall, 1935, *Ent. mon. Mag.* **71** : 61.

I have examined the type and two paratypes of this species and am satisfied that it is valid and easily recognised by the larger cuticular granules of Abd. VI, the anal spines and setae, and the form of the sense clubs in the sensory organ on Ant. III, which are very coarsely papillate (figs. 15 and 16).

The species is more or less as described by Bagnall but the following notes will also help in its identification :

Sensory organ on Ant. III with 5 papillae, 5 guard setae, 2 coarsely papillated sense clubs and 2 short plain sense rods close together ; the sense clubs arising from a deep chitinised pit (fig. 15).

Postantennal organ with 37–44 simple vesicles, touching and overlapping, and each showing a clear "circle of attachment", the whole organ appearing much as that in *P. magnicornis* (fig. 30).

Pseudocelli as follows :

Ant. base : 4 + 4, in 2 pairs close together in a row on each side.
Hind margin : 3 + 3 or 4 + 4, in a row.
Th. I : 1 + 1, lateral on each side.
Th. II : 3 + 3, being 2 dorsal and 1 lateral.
Th. III and Abd. I : 3 + 3, being 2 dorsal and 1 lateral.
Abd. II : 4 + 4, being 3 dorsal and 1 lateral.
Abd. III : 3 + 3, widely spaced.
Abd. IV : 5 + 5, being 3 diagonally placed close together and medial, and 2 lateral close together.
Abd. V : 3 + 3, close together diagonally placed.

Furcal ridge present, triangulate and marked by 4 rows of very short setae with 2, 2, 4 and 6 setae respectively.

Claw and unguiculus granulated basally, claw untoothed with long basal seta to each side; unguiculus long and tapering—whip-like, *not shorter* than claw (as stated by Bagnall) (fig. 13).

Clothing in the type and paratypes differs somewhat, probably owing to the poor condition of the specimens. The paratype is more heavily clothed with longer setae, arranged more or less in transverse rows across each body segment. In the type specimen the longer setae have been mostly lost except on the posterior region.

Anal spines on papillae : spines 26, papillae 3, hind claw 30.

Protaphorura stachi (Bagnall) (Figs. 17–20) **comb. nov.**

Onychiurus stachi Bagnall, 1935, *Vasculum* **21** : 102.

I have examined the type and one other specimen, presumably a paratype, of this species, which I regard as valid and fairly close to *O. debilis* Moniez.

Sensory organ on Ant. III as in figure 18, with rather globular shaped, coarsely granulated sense clubs and 2 short plain sense rods ; postantennal organ very similar in structure to that of *debilis* Moniez, but with 23–24 vesicles compared with 18 shown in *debilis* by Moniez and Denis and 20 by Folsom (*litoreus*).

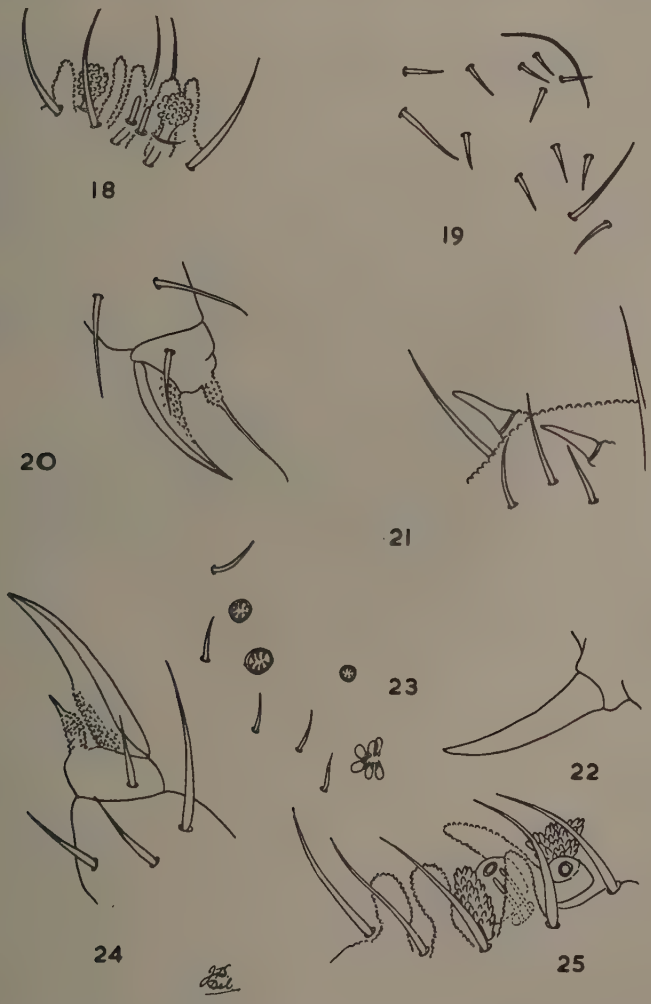
Pseudocelli as follows :

Ant. base : 3 + 3.
Hind margin : 2 + 2, obliquely placed.
Th. I : 1 + 1.
Th. II and III : 2 + 2.
Abds. I, II and III : 3 + 3, being 2 together diagonally placed and 1 lateral.

Abd. IV : 3 + 3, being 2 close together with a seta between them, and 1 removed diagonally placed.

Abd. V : 2 + 2, close together.

Two anal spines on papillae well separated, with associated setae as in figure 17. Spines 14, papillae 2, hind claw 20.



Figs. 18–25.—(18–20)—*Protaphorura stachi* (Bagnall), drawn from type: (18) sensory organ on Ant. III; (19) furcal ridge and setae; (20) hind claw. (21–25)—*Protaphorura moniezi* (Bagnall) drawn from type specimen of *moniezi*: (21) anal spines and associated dorsal setae; (22) anal spine from side; (23) pseudocelli of antennal base area and near end of postantennal organ; (24) hind foot; (25) sensory organ on Ant. III.

Claw and unguiculus distinctly granulated; claw without any teeth but with a very long basal seta to each side; unguiculus *not* as described by Bagnall, but with a short broad granulated basal inner lamella and a long filamentous extension overreaching the claw apex (fig. 20). (In *debilis* both Denis and Folsom show the unguiculus shorter than the claw.)

Rudimentary furca present, marked by a crescentic ridge and groups of short simple setae as in figure 19.

Protaphorura moniezi (Bagnall) (Figs. 21–25) **comb. nov.**

Onychiurus moniezi Bagnall, 1935, *Vasculum* **21** : 102.
Onychiurus evansi Bagnall, 1935, *Ent. mon. Mag.* **71** : 62, **syn. nov.**

For this species I examined the types of both *moniezi* and of *evansi*. I am satisfied that they are co-specific as, though each was examined independently, my notes on their morphology are identical.

The species *moniezi* is at once recognised by the peculiar dome-like accessory sense clubs in the sensory organ on Ant. III. I was very puzzled by these structures, but I saw them quite clearly as they are drawn in figure 25 on every occasion I examined the type specimen of *moniezi*. In fact, it was the presence of these structures in *evansi* that first suggested to me that the two species were one and the same.

P moniezi bears little resemblance to the descriptions given by Bagnall for either *moniezi* or *evansi*, and the following notes will give a clearer idea of it.

Length up to 1·25 cm.

Sensory organ on Ant. III with both granulated and dome-like sense clubs and 2 long, thin sense rods, 4 or 5 papillae and 5 guard setae (*moniezi* has 4 papillae on one antennal sense organ, 5 on the other; *evansi* has 5 on both). Postantennal organ with 18–22 broad, simple vesicles, touching and overlapping, and each with clear basal attachment thickenings, much as in *Spelaphorura thalassophilus* (fig. 64). Antennal base area not marked by smaller cuticular granules.

Pseudocelli as follows:

Ant. base: 3 + 3, as in fig. 23.
Hind margin: 2 + 2.
Th. I: 1 + 1.
Th. II: 1 + 1 or 3 + 3.
Th. III: 1 + 1 or 2 + 2.
Abd. I: 2 + 2, diagonally placed fairly close together.
Abd. II, III and IV: 2 + 2 or 3 + 3.
Abd. V: 3 + 3, arranged close together as an inverted triangle.

Anal spines and associated setae as in figure 21; anal spines 19–21, papillae 2–3, hind claw 28.

Furcal ridge absent.

Clothing rather sparse; the setae mostly short with occasional longer ones, mostly posteriorly.

Genital aperture in *evansi* type, conical and surrounded by whorls of very short setae numbering about 45 altogether, not seen in *moniezi* type.

Claw and unguiculus basally granulated; claw without teeth but with a long basal seta to each side; unguiculus short, with broad basal inner lamella and not reaching to half way down inner margin of claw.

Protaphorura furcifera (Börner) (Figs. 26–28) **comb. nov.**

Aphorura furcifera Börner, 1901, *Abh. naturw. Ver. Bremen* **17** : 3; *Ibid.* **17** : 22.

Onychiurus celticus Bagnall, 1935, *Scot. Nat.* **1935** : 89, **syn. nov.**
Onychiurus scoticus Bagnall, 1935, *Ent. mon. Mag.* **71** : 63, **syn. nov.**

Examination of the type of this species from the Carl Börner Collection in the British Museum (Natural History) shows it to be as described by Börner but, as he gave figures of the furcula only in a subsequent publication, the accompanying drawings made from his type specimen may be of interest and value.

Remarks : In connection with Bagnall's species I have examined the type, five paratypes and three other specimens of *O. scoticus* Bagnall, and three specimens labelled *O. celticus* Bagnall.

These three specimens of *celticus* are not marked as types but presumably are the specimens upon which Bagnall based his 1935 description. The labels on these three slides bear the name *scoticus* crossed out and *celticus* written in in Bagnall's handwriting—"*Dalmeny Estate II :* 35". The specimens of *celticus* each have a very minute fully formed furcula and agree in all other morphological details with the type of *furcifera*. The furcula cannot be seen on the type specimen of *scoticus* nor on three of the other specimens—two from Gleneagles and one from Garrock. In other morphological details, however, they are like those in which the furcula is visible and are, I think, correctly identified as *furcifera*.

Protaphorura magnicornis (Bagnall) (Figs. 29–31) **comb. nov.**

Onychiurus magnicornis Bagnall, 1935, *Scot. Nat.* **1935** : 88.

I have examined the type and a paratype of this species.

Length up to 1·75 mm.

Sensory organ on Ant. III marked by strongly chitinised integumentary fold and with 5 papillae, 5 guard setae, one of which is exceptionally long and stout, 2 large coarsely granulate sense clubs and a pair of long thin curved sense rods (fig. 29). Postantennal organ with 40–42 touching and overlapping vesicles, each with distinct chitinised basal "rings" of attachment (fig. 30). Antennal base area distinct with smaller granules.

Pseudocelli as follows :
Ant. base : 2 + 2.
Hind margin : 3 + 3.
Th. I : 0 + 0.
Th. II : 1 + 1.
Th. III : 2 + 2, separated.
Abds. I–V : with 3 + 3 each.

Anal spines stout and faintly curved, separated and mounted on small papillae. Spines 19, papillae 3, hind claw 29 on type ; 27, 5, 39 respectively on paratype.

Furcal ridge present, very rudimentary and marked by two transverse curved rows of short curved setae, the anterior row of 3, the posterior row of 6 setae.

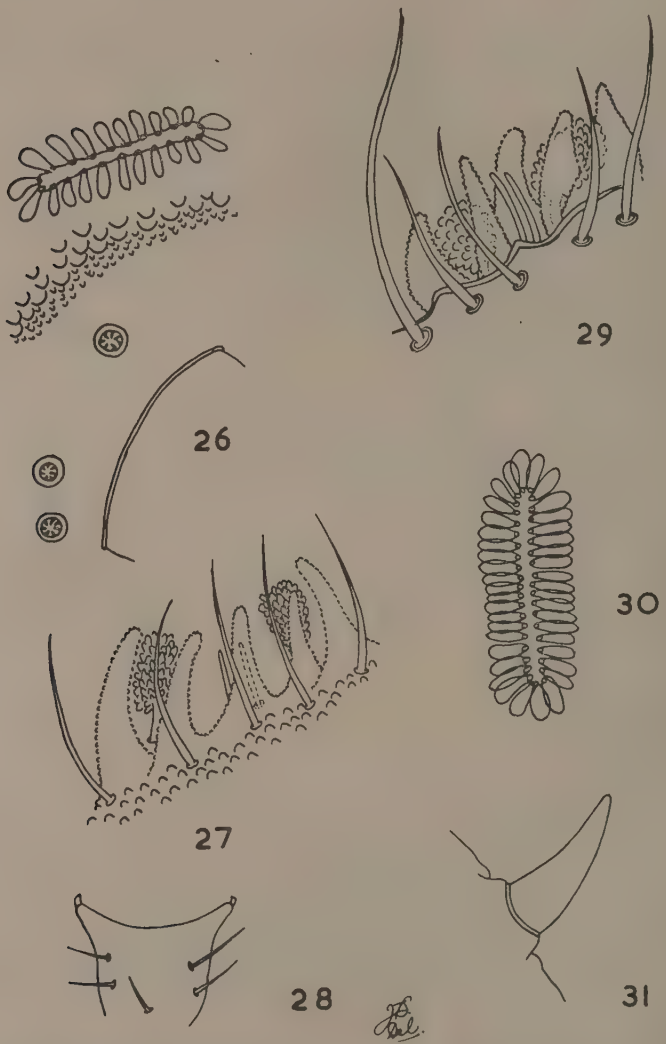
Clothing, moderate, of short (occasional longer) setae, the latter more especially posteriorly. Claw toothed, similar to that of *P. armata denticulata* (fig. 12) and with a moderately long basal seta to each side ; unguiculus tapering with filamentous extension reaching to apex of claw or *slightly* beyond.

This species seems quite distinct by virtue of the pseudocelli of the antennal base area being clearly only two, and by the nature of the postantennal organ and structure of the foot.

Protaphorura halophila (Bagnall) (Figs. 32–36) **comb. nov.**

Onychiurus littoralis Bagnall, 1935, *Scot. Nat.* **1935** : 114, **syn. nov.**
Onychiurus halophilus Bagnall, 1937, *Scot. Nat.* **1937** : 89.

Of this species I have examined the type, one paratype and two other specimens from the type locality.



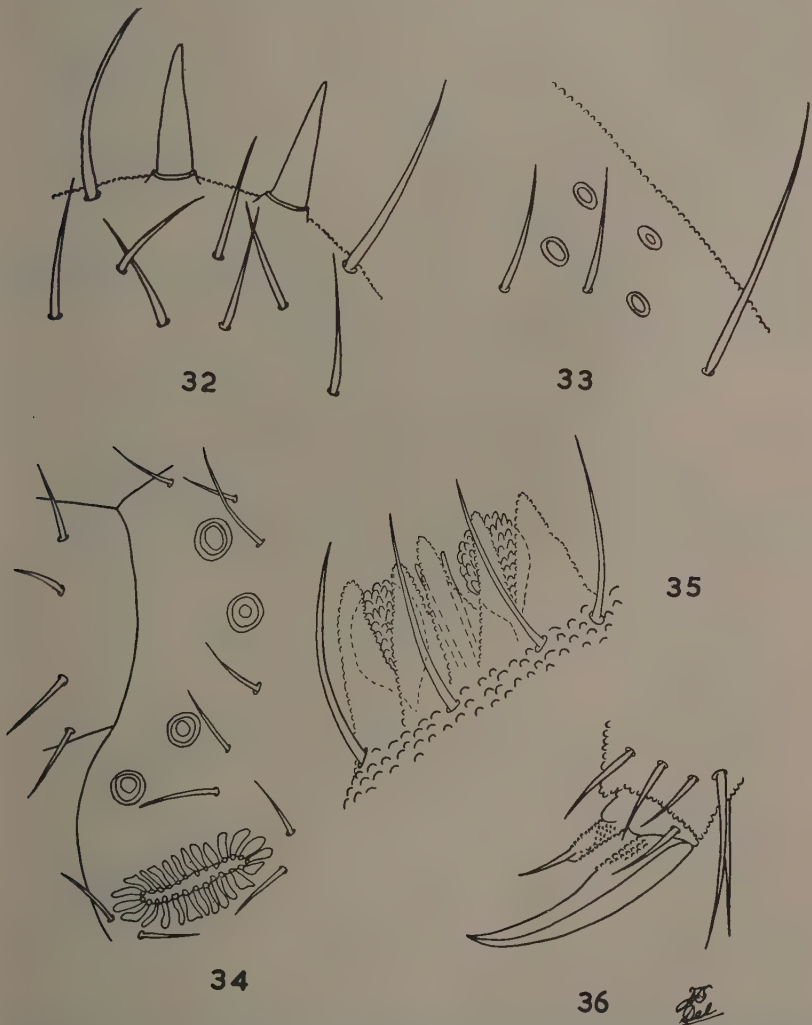
Figs. 26–31.—(26–28)—*Protaphorura furcifera* (Börner), drawn from type: (26) post-antennal organ and pseudocelli of antennal base area; (27) sensory organ on Ant. III; (28) furcula. (29–31)—*Protaphorura magnicornis* (Bagnall), drawn from type: (29) sensory organ on Ant. III; (30) postantennal organ; (31) anal spine from side.

Sensory organ on Ant. III with 5 papillae, 4 guard setae, 2 large, globular granulated sense clubs and a pair of long thin sense rods (fig. 35). Postantennal organ of typical *armata* type, and consisting of 24–30 vesicles with their basal attachment " circles " quite distinct.

Pseudocelli as follows :

Ant. base : 4 + 4, arranged as in figure 34.

Hind margin : 4 + 4, arranged as in figure 33, *not* 3 + 3, as originally described by Bagnall.



FIGS. 32–36.—*Protaphorura halophila* (Bagnall), drawn from paratypes : (32) anal spines and associated dorsal setae ; (33) pseudocelli from hind margin of head ; (34) post-antennal organ and antennal base area with pseudocelli ; (35) sensory organ on Ant. III ; (36) hind foot.

Th. I : 1 + 1.

Th. II and III : 2 + 2, diagonally placed.

Abd. I : 4 + 4, fairly close together in a crescent shaped row.

Abd. II : 3 + 3, arranged as a triangle, apex directed posteriorly, or in a curved transverse row.

Abd. III : 3 + 3, 4 + 4 or 5 + 5, in a curved, transverse row curving towards the anterior.

Abd. IV : 4 + 4, in a row, or three in a triangle, apex directed anteriorly, and the fourth lateral.

Abd. V : 4 + 4, or 5 + 5, three close together in a row and one or two removed laterally.

Anal spines on short papillae, the spines pointed, more or less straight and with associated setae as in figure 32. Spines 23, papillae 3, hind claw 38.

Furcal ridge present and marked by 4 irregular rows of very short setae arranged with 3, 7–9, 5–7 and 3 setae in each row.

Claw and unguiculus granulated basally ; claw without teeth but with a very long basal seta to each side ; unguiculus with stout basal granulated half and apical needle-like extension, the whole reaching to about two-thirds down claw.

Clothing of mostly short, simple setae, longer posteriorly.

This species appears to be quite distinct, though related on the one hand to *octopunctata* (Tullb.) in the structure of the postantennal organ and the presence of furcal rudiments, and on the other to *litoreus* Folsom in the presence of pseudocelli on Th. I and through the short unguiculus.

Protaphorura tullbergi (Bagnall) (Figs. 37–43) **comb. nov.**

Onychiurus tullbergi Bagnall, 1937, *Scot. Nat.* **1937** : 115.

I have examined three paratypes of this species.

Sensory organ on Ant. III (fig. 40) very similar to that of *P. halophila*. Postantennal organ with 26–30 vesicles (not 36 as described by Bagnall), of typical *armata* form with distinct basal thickened attachment zones. Antennal base area distinct, with finer granules.

Pseudocelli as follows :

Ant. base : 3 + 3, arranged as in figure 38.

Hind margin : 2 + 2, not 3 + 3, as described by Bagnall.

Th. I : 0 + 0.

Th. II and III : 1 + 1.

Abd. I, II and III : 3 + 3, being 2 dorsal, not very close, and one lateral in each case.

Abd. IV : 3 + 3, being 2 close together diagonally and one removed.

Abd. V : 2 + 2, the two pseudocelli of each side guarded by 3 setae as shown in figure 42. In general the arrangement of the pseudocelli is as originally described by Bagnall.

Anal spines and associated setae as shown in figure 43. Spines 25, papillae 5, hind claw 32.

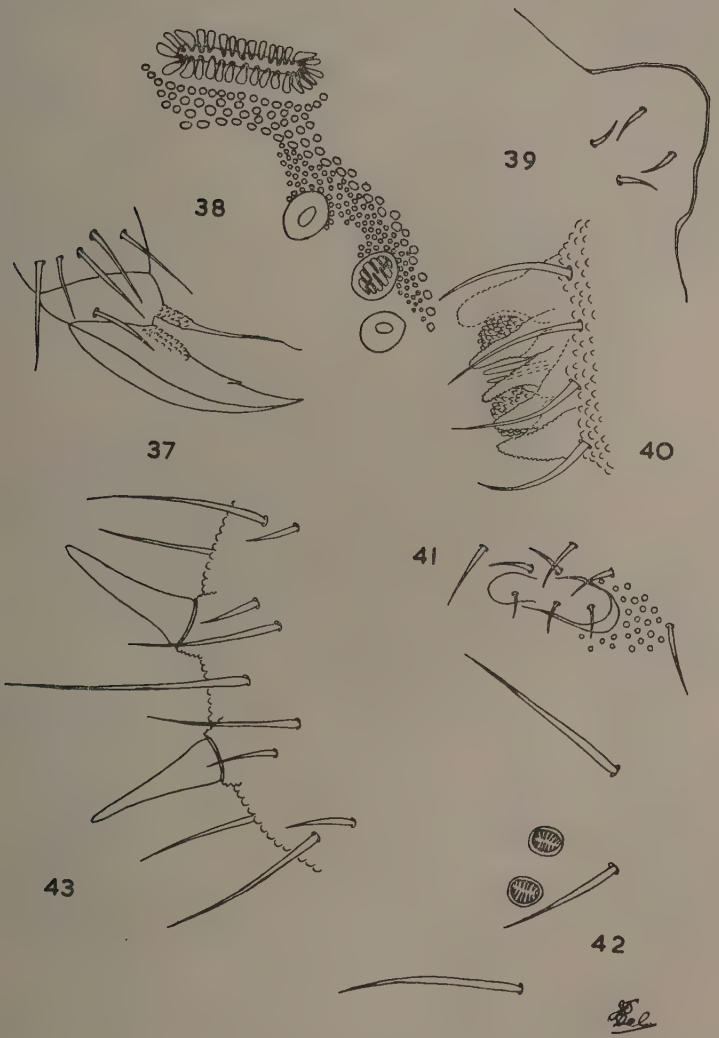
Furcal rudiments present as distinct integumentary ridge bearing 4 short setae (fig. 39).

Claw (fig. 37) with strong inner tooth below centre, no outer teeth ; a long basal seta to each side ; unguiculus tapering and reaching to level of apex of claw on hind feet, but slightly shorter on other feet ; both claw and unguiculus granulate dorsally.

Genital aperture of female as in figure 41 ; that of the male with 10–12 short setae arranged irregularly in transverse rows anterior to pore, 3 minute setae inside lip of pore and the 2 longer flanking setae further removed.

Clothing of short setae with occasional longer ones posteriorly ; the short setae mostly in ill-defined transverse rows.

As suggested by Bagnall, this species is probably closest to *P. octopunctata* (Tullb.)

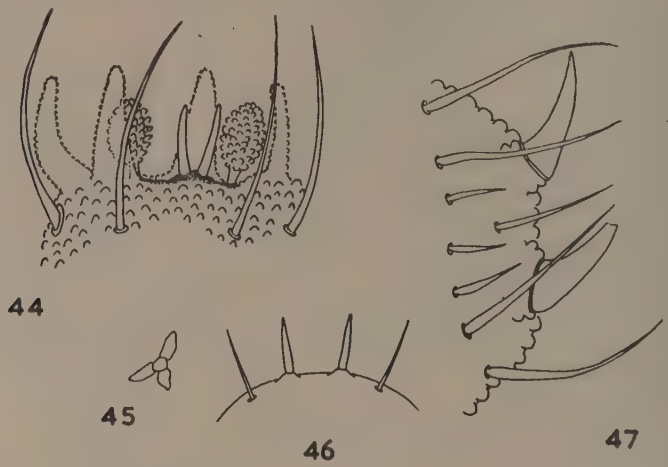


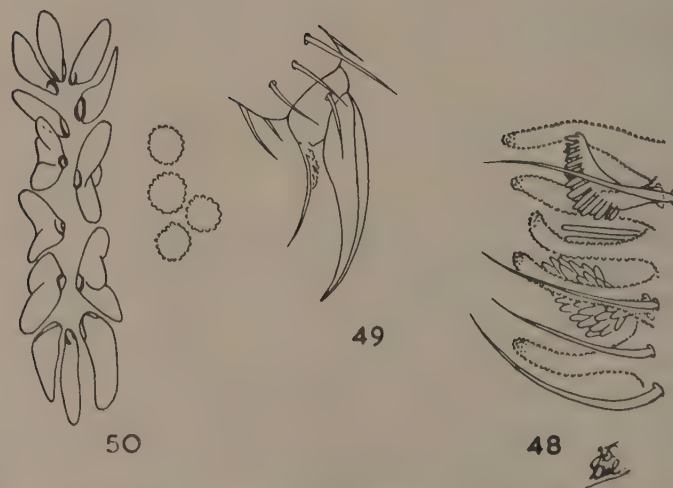
Figs. 37–43.—*Protaphorura tullbergi* (Bagnall), drawn from paratypes: (37) hind foot; (38) postantennal organ and pseudocelli of antennal base area; (39) furcal ridge; (40) sensory organ on Ant. III; (41) female genital aperture; (42) pseudocelli of one side of Abd. V with the three guarding setae; (43) anal spines and associated dorsal setae.

Arcaphorura absoloni (Börner) (Figs. 44–46) **comb. nov.**

Aphorura absoloni Börner, 1901, *Zool. Anz.* **24** : 422.
Micraphorura handschini Bagnall, 1949, *Ann. Mag. nat. Hist.* (12) **2** : 510, **syn. nov.**

The type of this species is in the Carl Börner Collection in the British Museum (Natural History). The species is substantially as described by Börner, and the three figures included here are prepared from the type.





Figs. 44–50.—(44–46)—*Arcaphorura absoloni* (Börner), drawn from type: (44) sensory organ on Ant. III; (45) postantennal organ; (46) anal spines from above. (47–50)—*Hymenaphorura subsimilis* (Bagnall), drawn from type: (47) anal spines and associated dorsal setae; (48) sensory organ on Ant. III; (49) hind foot; (50) postantennal organ and some nearby cuticular granules.

Sense rods in sensory organ on Ant. III behind a strongly chitinised ridge (fig. 44). Claw without teeth; unguiculus lanceolate, about one-fourth to one-third length of claw. Clothing very sparse, of short simple setae, longer posteriorly. Length 0·7 mm.

The species *Micraphorura handschini*, erected by Bagnall for the specimens which Handschin described as *O. absoloni* Börner from Switzerland (1920, *Ver. naturf. Ges. Basel* **32** : 9), is untenable in my opinion. The differences in pseudocelli cited by him as the grounds for the erection of the species are insufficient to be used as specific characters without careful study and comparison of the actual specimens upon which Börner's and Handschin's descriptions were based. The differences cited by Bagnall could be due to errors in observation by either Börner or Handschin. The figures given by Handschin of the sensory organ on Ant. III and the postantennal organ from his specimens agree extraordinarily closely with the figures I have drawn of these structures from Börner's type specimen, even to the chitinous ridge in front of the sense rods in the sensory organ on Ant. III. I consider, therefore, that Bagnall's species *handschini* is a synonym of Börner's original species *absoloni*.

Hymenaphorura subsimilis (Bagnall) (Figs. 47–50) **comb. nov.**

Onychiurus subsimilis Bagnall, 1948, *Ann. Mag. nat. Hist.* (11) **14** : 637.

I have examined the type of this species and consider it valid and closely related to *H. similis* (Folsom).

Sensory organ on Ant. III with 5 rather tall narrow curved papillae, 4 guard setae, 2 large curved strongly papillate sense clubs and a pair of tall, narrow sense rods (fig. 48). (The cuticular fold mentioned by Bagnall in his original description is present, though possibly an artifact produced in mounting, but I can find no trace of his knobbed processes.) Postantennal organ with 12–13 simple or lobed vesicles with distinct thickened attachment " zones ", as in figure 50 (Bagnall gave 8–10 vesicles in his original description). Antennal base area distinct, with very small cuticular granules. Each body segment with similar small cuticular granules arranged across the anterior and posterior borders as narrow, transverse bands; the larger cuticular granules between them largest on Abds. V and VI.

Pseudocelli as follows :

Ant. base : 1 + 1.

Hind margin : 0 + 0.

Th. I : 0 + 0.

Th. II : 1 + 1, small, not much larger than 2–3 cuticular granules.

Th. III, Abds. I–V : 1 + 1 each, small but not quite so small as those of Th. I.

Anal spines curved, on papillae, with associated setae as in figure 47. Spines 20, papillae 5, hind claw 17.

Clothing moderate, of short setae with much larger ones posteriorly.

Claw granulate basally, without teeth, but with a moderately long slender basal seta to each side; unguiculus needle-like with granulated inner lamella (fig. 49). Length to 1·25 mm.

Metonychiurus michelbacheri (Bagnall) (Figs. 51–53) **comb. nov.**

Onychiuroides michelbacheri Bagnall, 1948, *Ann. Mag. nat. Hist.* (11) **14** : 642.

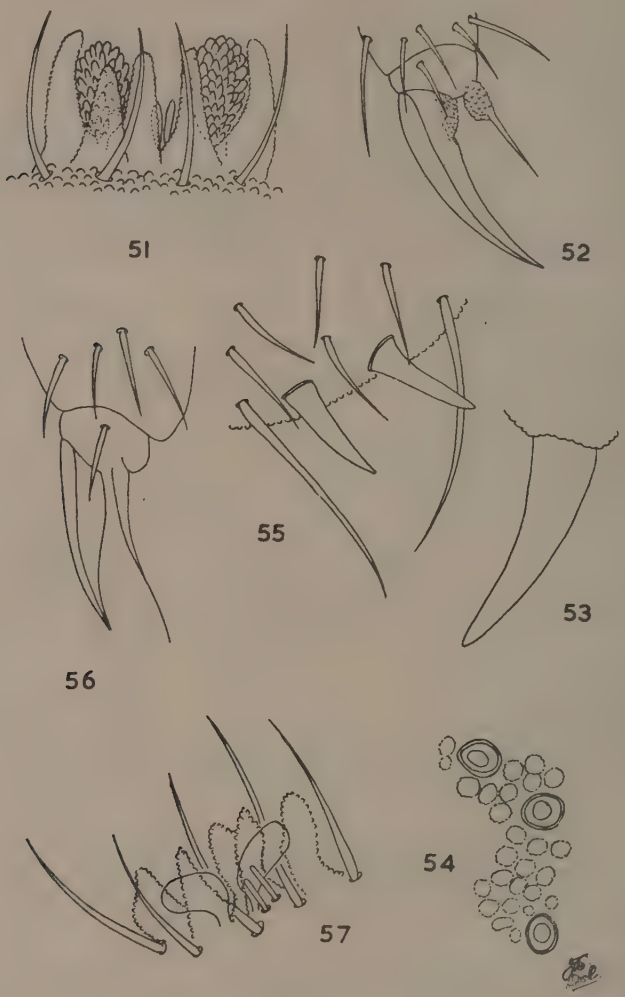
I have examined the type and one paratype of this species.

Sensory organ on Ant. III characterised by 2 very large, coarsely granulate, almost papillate, sense clubs, as high as or slightly higher than the 5 granulated papillae (fig. 51); 2 comparatively short, stoutish sense rods and 4 guard setae complete the organ.

Postantennal organ entirely absent.

Pseudocelli as follows :

Ant. base : 3 + 3, arranged more or less in a triangle with its apex directed outwards, very small (not larger than 3 cuticular granules and hence very difficult to see) ; the chitinous borders present but very narrow.



Figs. 51–57.—(51–53) —*Metonychiurus michelbacheri* (Bagnall), drawn from type : (51) sensory organ on Ant. III ; (52) hind foot ; (53) anal spine from side. (54–57)—*Handschiniella bagnalli* sp. n., drawn from type : (54) pseudocelli of antennal base area ; (55) anal spines and associated dorsal setae ; (56) hind foot ; (57) sensory organ on Ant. III.

Hind margin : 1 + 1, the type only with 2 on one side.
Th. I : 1 + 1.
Th. II and III : 2 + 2.
Abd. I : 1 + 1.
Abd. II : 2 + 2, well separated.
Abd. III : 3 + 3, being 2 together transversely and one removed.
Abd. IV : 3 + 3, being 2 together diagonally and one removed.
Abd. V : 1 + 1 in type, 3 + 3 in paratype.

I can find no trace of the spine-like setae Bagnall mentions as associated with the pseudocelli of Abd. V.

Anal spines well separated, slightly curved, tapering and on papillae. Spines 25, papillae 5, hind claw 25.

Genital aperture conical and surrounded by many short setae.

Clothing sparse, of short setae and moderately long setae posteriorly.

Claw without teeth, but with swollen basal inner ridge and a long basal seta to each side ; both claw and unguiculus coarsely granulate basally ; the unguiculus bulbous basally, with needle-like extension reaching to about two-thirds down claw (fig. 52). Length up to 1·6 mm.

The type specimen is reasonably well preserved but it is not possible to diagnose the arrangement of the setae associated with the anal spines. The paratype is badly damaged in the posterior region.

Spelaphorura glenniei Bagnall (Figs. 58–62)

1948, *Ann. Mag. nat. Hist.* (11) **14** : 639.

I have examined the type and two paratypes of this species.

Ant. IV with subapical pit containing small sense club and with numerous curved sensory setae. Sensory organ on Ant. III (rather inadequately described by Bagnall) as in figure 61 ; detailed structure of sense clubs with their " bent and twisted lamellae " and the pair of sense rods shown in figure 62. Postantennal organ, visible in its entirety only on one side of the type specimen, as shown in figure 60. Bagnall's estimate of 70–90 vesicles probably about correct. Vesicles narrow and elongate, set at right angles to the long axis of the organ, the detail of their insertions shown in figure 59. (In the paratypes some of the vesicles are widely separated but I think this may have resulted from Bagnall's extremely rough mounting of the specimens.)

Pseudocelli as follows :
Ant. base : 4 + 4, being 3 in line and 1 above on inner edge.
Hind margin : 6 + 6, being an inner triangle, apex directed anteriorly, and an outer row of 3.
Th. I : 7–8 + 7–8, mostly laterodorsal.
Th. II : 8–9 + 8–9, mostly laterodorsal.
Th. III : 6–7 + 6–7.
Abd. I : 8–9 + 8–9.
Abd. II : 9 + 9.
Abd. III : 7–8 + 7–8.
Abd. IV : 4–5 + 4–5.
Abd. V : 3–4 + 3–4.

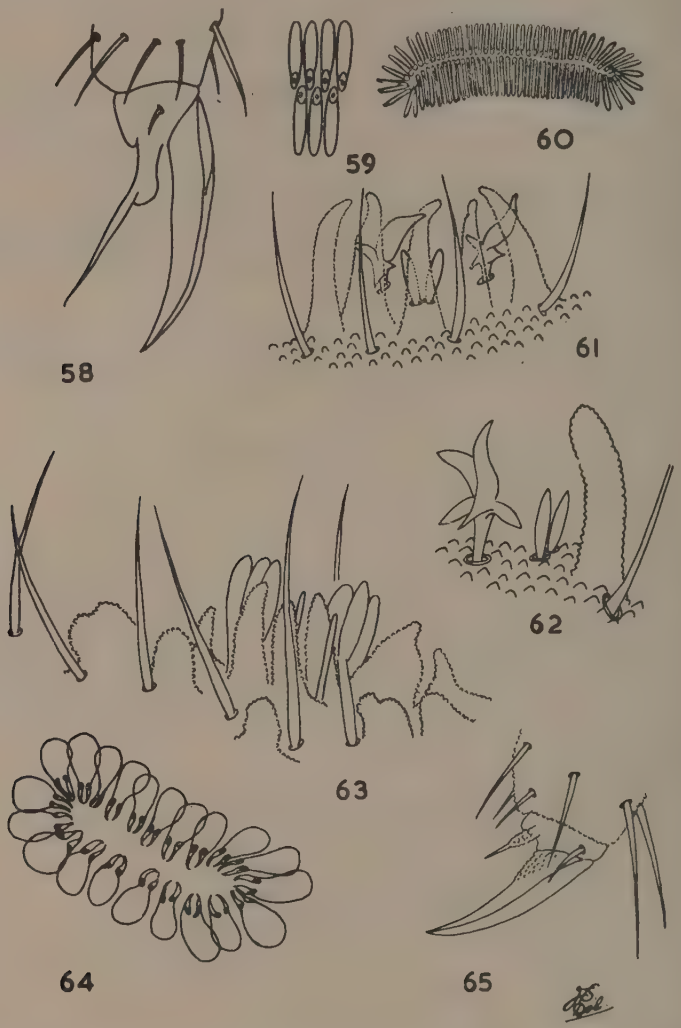
Body pseudocelli mostly rather irregularly arranged. (They are very clear on the type specimen but not so clear on the other ; it would appear that their numbers are very variable.)

Genital aperture guarded by 4 irregular rows of short setae, about 28 altogether.

Furcal rudiments absent ; anal spines absent.

Length up to 2·5 mm., not 4 mm., as stated by Bagnall. Antennal segments related as 16 : 30 : 20 : 79.

Clothing heavy, of moderately long setae. Claw with a pair of outer lateral teeth about one-quarter to one-third down, no inner teeth, but a very short basal seta to each side;



Figs. 58–65.—(58–62) *Spelaphorura glenniei* Bagnall, drawn from type: (58) hind foot; (59) detailed structure of vesicles from postantennal organ; (60) postantennal organ; (61) sensory organ on Ant. III; (62) sectional view of sensory organ on Ant. III to show detailed form of sense club. (63–65)—*Spelaphorura thalassophilus* (Bagnall), drawn from paratypes: (63) sensory organ on Ant. III; (64) postantennal organ; (65) hind foot.

unguiculus needle-like, reaching almost to level of apex of claw and with a broad, distally swollen, inner lamella (fig. 58).

Spelaphorura thalassophilus (Bagnall) (Figs. 63–65) **comb. nov.**

Onychiurus thalassophilus Bagnall, 1937, *Scot. Nat.* **1937** : 146.
Onychiurus imminutus Bagnall, 1937, *Scot. Nat.* **1937** : 146, **syn. nov.**

I have examined two paratypes of *thalassophilus* and the type of *imminutus* and I consider them to be one and the same species.

Sensory organ on Ant. III with the 2 sense clubs longitudinally lamellated, giving them a characteristic petallate or " tulip-like " appearance. This organ was not mentioned in Bagnall's original description, but, in addition to the two sense clubs, 2 long thin, widely separated sense rods, 12–13 low papillae of varying shapes, as shown in figure 63, and 6 guard setae present. Postantennal organ quite unlike Bagnall's original description, being composed of 20–24 broad vesicles, often touching or overlapping and each with 2 very distinct basal chitinous thickenings (fig. 64).

Pseudocelli as follows :

Ant. base : 3 + 3, in a broad triangle, apex directed posteriorly.
Hind margin : 2 + 2.
Th. I : 1 + 1.
Th. II : 2 + 2, transversely.
Th. III ; Abd. I and II : 2 + 2, diagonally.
Abd. III : 3 + 3, in a short crescent.
Abd. IV : 3 + 3, being one behind another and the third towards the outer side, giving an L-shape.
Abd. V : 2 + 2.

Anal spines present, almost straight and on well separated papillae. Spines 17, papillae 5, hind claw 29.

Genital aperture flanked by two small, widely spaced papillae, each of which is covered by numerous short setae. Furcal rudiments entirely absent.

Clothing sparse, of short curved setae.

Claw basally granulate, without teeth, but with a long basal seta to each side ; unguiculus not " reduced to a minute stumpy process " as stated by Bagnall, for, although reduced, it is fully developed with a stout basal granulated section bearing a sharp needle-like process, the whole reaching to about one-third down inner margin of claw.

Length to 1·3 mm.

Bagnall related this species to *O. debilis* which is, of course, absurd. It appears to be quite unique. The type of *imminutus* is in very bad condition, having been squashed almost beyond recognition as an insect. However, amongst the debris I managed to locate a postantennal organ with the three adjacent pseudocelli, the two antennae and several feet, sufficient to establish its identity with *thalassophilus*.

Absolonia gigantea (Absolon) (Figs. 66–68)

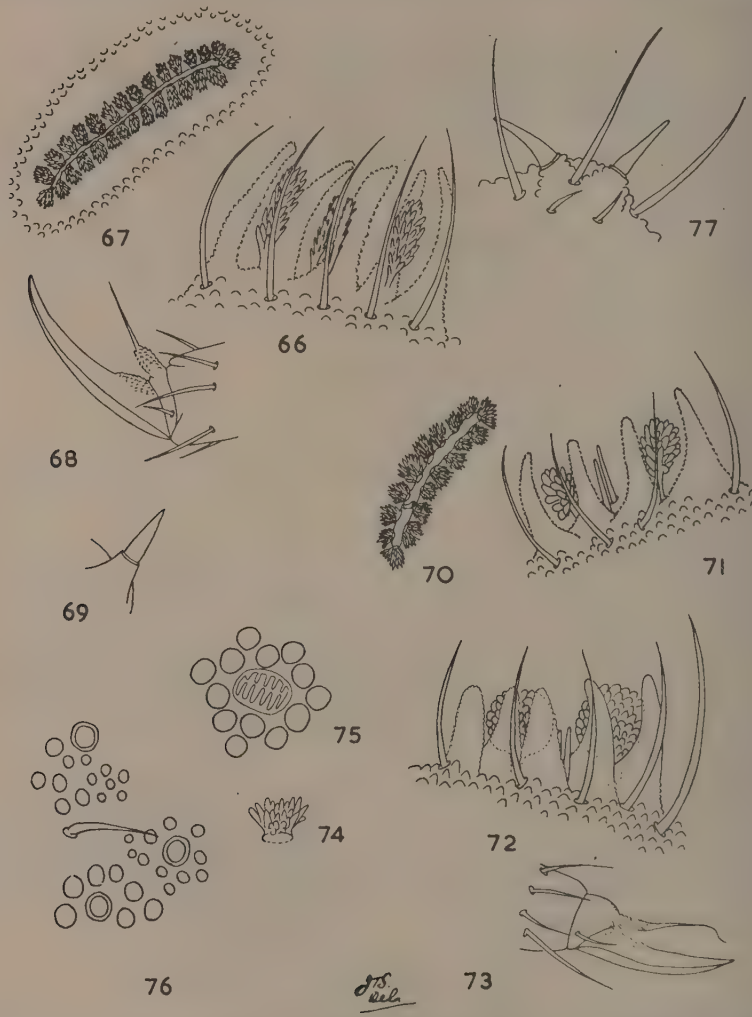
Aphorura gigantea Absolon, 1901, *Zool. Anz.* **24** : 85.
Absolonia gigantea Absolon, Börner, 1901, *Zool. Anz.* **24** : 357.

Four specimens of this species from the type locality collected in 1937, and now in the British Museum (Natural History), may be regarded as correctly identified and as examples of the type species of the genus *Absolonia*. The following notes may serve in the future identification of this species.

Length up to 3·3 mm.

Clothing sparse, of short simple setae.

Sensory organ on Ant. III as shown in figure 66, with pair of sense rods serrated rather than granulated, as has been generally accepted. The two sense clubs long, narrow and strongly granulated, almost papillated ; the papillae more or less normal, only one appearing



FIGS. 66–77.—(66–68) *Absolonia gigantea* (Absolon), drawn from specimen in Börner Collection, possibly a paratype : (66) sensory organ on Ant. III ; (67) postantennal organ ; (68) hind foot. (69–71) *Paronychiurus conjungens* (Börner), drawn from type : (69) anal spine from side ; (70) postantennal organ ; (71) sensory organ on Ant. III. (72–77)—*Kalaphorara bearei* (Bagnall), drawn from type : (72) sensory organ on Ant. III ; (73) hind foot ; (74) vesicle from postantennal organ ; (75) pseudocellus from antennal base area ; (76) pseudocelli on antennal base with cuticular granules and guard seta ; (77) anal spines and associated setae.

at all truncated ; the 5 guard setae normal. Apex of Ant. IV with sensory pit and knob. Postantennal organ with 29 compound tuberculated vesicles (fig. 67), the whole in a finely granulated deep, cuticular groove.

Pseudocelli as follows :

Ant. base : 3 + 3, being 2 on the base area and 1 off, all widely separated.

Hind margin : 3 + 3, as a triangle, with inner two close together, one above the other, and third removed slightly laterally.

Th. I : 1 + 1.

Th. II : 2 + 2.

Th. III and Abd. I : 3 + 3, two close together diagonally and the third more lateral.

Abd. II : 2 + 2.

Abds. III and IV : 3 + 3, more or less in line.

Abd. V : 2 + 2, rather diagonally placed.

Claw and unguiculus granulate basally, the claw with a moderate to short basal seta to each side and without teeth ; unguiculus basally cone-shaped with a long, straight, needle-like extension reaching to about two-thirds down inner edge of claw (fig. 68).

Paronychiurus conjungens (Börner) (Figs. 69–71) **comb. nov.**

Protaphorura conjungens Börner, 1909, *S.B. Ges. naturf. Fr. Berl.* **1909** : 104.

I have examined the type of this species from the Börner Collection in the British Museum (Natural History) and it is substantially as described by Börner in 1909 but, as he gave no illustrations, the accompanying figures drawn from the type specimen, may be of some value. It should be noted that I have found the sense clubs of the sensory organ on Ant. III very coarsely granulate, almost papillate, and not finely granulate.

Paronychiurus edinensis (Bagnall) (Figs. 82–84) **comb. nov.**

Onychiurus edinensis Bagnall, 1935, *Scot. Nat.* **1935** : 117.

I have examined two paratypes of this species, which proves to be valid.

Sensory organ on Ant. III with 5 papillae, 5 guard setae, 2 elongate, coarsely granulate, almost papillate sense clubs, and a pair of long, thin, tapering sense rods (fig. 84).

Postantennal organ compound, consisting of 14–15 tuberculated vesicles (fig. 83).

Pseudocelli as follows :

Ant. base : 3 + 3, as in figure 83.

Hind margin : 2 + 2.

Th. I and II : 2 + 2.

Th. III : 3 + 3.

Abd. I and II : 1 + 1.

Abd. III : 3 + 3.

Abd. IV : 4 + 4.

Abd. V : 3 + 3, dorsally with 2 pairs of short spine-like setae.

Abd. VI : with 2 rather long, curved, widely separated anal spines, without papillae, the spines about 1·25 times as long as the hind claw.

Claw without teeth but with a moderately long, broad seta to each side ; both claw and unguiculus granulate basally, the unguiculus lanceolate, reaching about half way down inner edge of claw.

Clothing sparse, of short setae with some longer ones posteriorly. Length up to 1·2 mm.

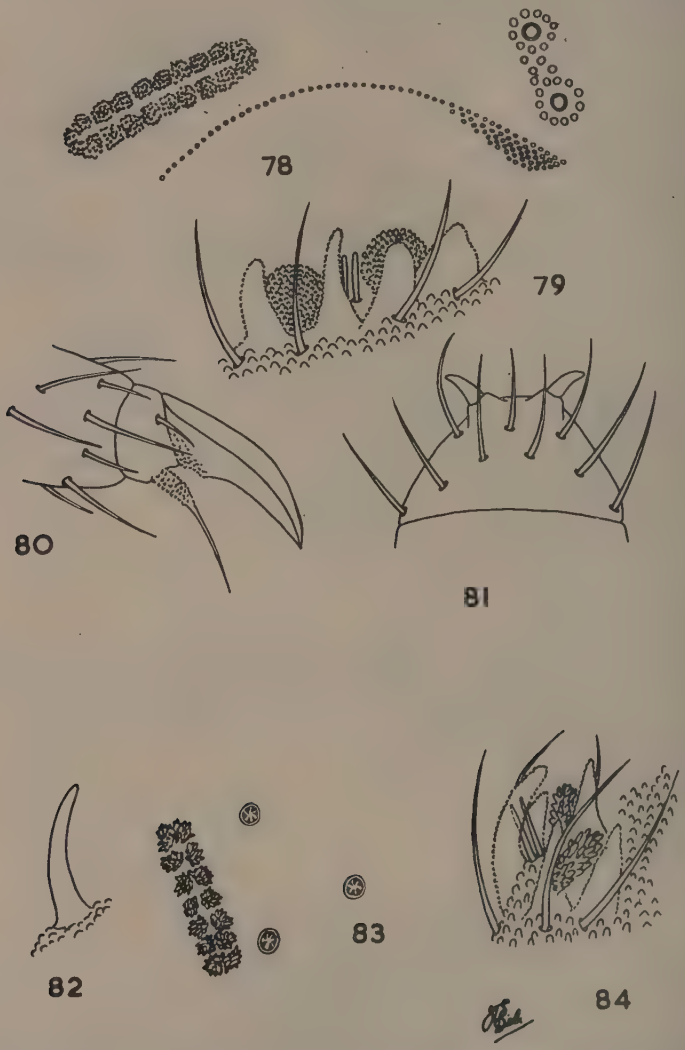
Kalaphorura bearei (Bagnall) (Figs. 72–77) **comb. nov.**

Onychiurus bearei Bagnall, 1937, *Scot. Nat.* **1937** : 148.

I have examined the type of this species which I consider is correctly placed

in the genus *Kalaphorura*, as the pseudocelli are exceedingly small and show no distinct chitinous borders (fig. 75).

Sensory organ on Ant. III with 5 papillae, 5 guard setae, 2 large, globular, coarsely granulated sense clubs and a pair of short, tapering, straight sense rods (fig. 72). Ant. IV



FIGS. 78–84.—(78–81) *Paronychiurus millsi* sp. n., drawn from type: (78) postantennal organ, antennal base area and the two associated pseudocelli; (79) sensory organ on Ant. III; (80) hind foot; (81) Abd. VI showing anal spines and associated dorsal setae. (82–84) *Paronychiurus clincnsis* (Bagnall), drawn from paratype: (82) anal spine from side; (83) postantennal organ and pseudocelli of antennal base area; (84) sensory organ on Ant. III in side view.

with subapical pit containing a small sense club. Postantennal organ consisting of 12–16 compound vesicles, as in *O. fimetarius*, lying in a deep integumentary groove having very small cuticular granules. Cuticular granules of head abnormally large.

Pseudocelli very difficult to see, being extremely small and not much larger than 2–3 cuticular granules (fig. 76) arranged as follows:

Ant. base: 3 + 3, as in fig. 76.
Hind margin: 2 + 2.
Th. I: 1 + 1.
Th. II: 1 + 1.
Th. III: not visible, possibly 0 + 0.
Abd. I: 1 + 1.
Abds. II, III and IV: 2 + 2, widely spaced.
Abd. V: 2 + 2, close together diagonally.

Antennal base area clearly marked by smaller cuticular granules, of about same size as those on thorax and abdomen.

Anal spines slightly curved, on large papillae, and with associated setae, as in figure 77. Spines 36, papillae 19, hind claw 43.

Claw and unguiculus both granulate basally; claw without teeth, but with a long basal seta to each side; unguiculus long and tapering with filamentous extension to apex of claw.

Furcal rudiments not visible, probably absent. Clothing conspicuous, of mostly very long setae and occasional shorter ones. Length 0·9 mm.

Onychiurus fimetarius L.

Onychiurus pygmaeus Bagnall, 1937, *Scot. Nat.* **1937**: 146, **syn. nov.**

I have examined paratypes of Bagnall's species *pygmaeus*, and found that the pseudocelli are not as described by him but are typical in number and arrangement of *O. fimetarius* L.

The sensory organ on Ant. III and the postantennal organ of *pygmaeus* are as found in *fimetarius*. The unguiculus in *pygmaeus* is not as long as that shown for European species of *O. fimetarius* by Stach, but shorter, as drawn by Folsom for North American species. I have no hesitation in placing *O. pygmaeus* Bagnall as a synonym of *O. fimetarius* L.

Onychiurus ambulans (Nicolet)

Onychiurus laminatipes Bagnall, 1937, *Scot. Nat.* **1937**: 148, **syn nov.**

Amongst the Bagnall slides was one labelled *O. laminatipes* from Micheltown Cave, which on examination proved to be none other than *O. ambulans* (Nic.). This specimen would undoubtedly be cospecific in Bagnall's mind with the new species *O. laminatipes* which he erected in 1937 for Handschin's specimens of *O. ambulans* (1920, *Verh. naturf. Ges. Basel* **32**: 23). I do not think Bagnall was justified in giving Handschin's specimens the new name *laminatipes* in the way he did and, as the slide in his collection bearing this name is undoubtedly *O. ambulans*, I would sink his name *laminatipes* as a synonym of *O. ambulans* (Nic.).

Hymenaphorura alticola (Bagnall) **comb. nov.**

Onychiurus alticola Bagnall, 1935, *Ent. mon. Mag.* **71**: 63.
Onychiurus sibiricus Handschin, 1920, *Verh. naturf. Ges. Basel* **32**: 14.

The two species *H. troglodytes* and *O. alticola* were discussed by Stach (1954 : 99–101), who showed conclusively that the name *alticola* must now be used for Handschin's specimens of *O. sibiricus* from Switzerland, which must therefore now be known as *Hymenaphorura alticola* (Bagnall).

Hymenaphorura sibirica (Tullberg)

Hymenaphorura troglodytes Bagnall, 1948, *Ann. Mag. nat. Hist.* (11) **14** : 637.

Stach (1954 : 100) also shows the name *troglodytes* to be a synonym of *H. sibirica* (Tullb.).

Paronychiurus spinosus (Bagnall) **comb. nov.**

Onychiuroides spinosus Bagnall, 1949, *Ent. mon. Mag.* **85** : 51.

No specimens were present in Bagnall's collection and so, for the present, this species must be left in the literature, but transferred to the genus *Paronychiurus*.

Arcaphorura quadrituberculatus (Börner) **comb. nov.**

Onychiurus quadrituberculatus Börner, 1901, *Abh. naturf. Ver. Bremen* **17** : 23.
Dimorphaphorura differens Bagnall, 1949, *Ann. Mag. nat. Hist.* (12) **2** : 511, **syn. nov.**
Onychiurus quadrituberculatus Stach, 1947, *Acta Mus. Hist. nat. Krakow* **7** : 10.

Bagnall's species *differens*, founded on the literature, would not appear, on examination of the relevant publications, to be a valid species. Stach (1947 : 12), in discussing Börner's *quadrituberculatus* and other related species, points out that a certain amount of variation in body structures occurs. Bagnall, for instance, in giving the number of vesicles in the postantennal organ of Stach's specimens as part of his reason for erecting the species *differens*, ignores Stach's statement that the postantennal organ consists of "usually three, rarely four peripheral tubercles". This is again discussed by Stach in his 1954 monograph (page 70).

Protaphorura discrepans (Bagnall) **comb. nov.**

Dimorphaphorura discrepans Bagnall, 1949, *Ann. Mag. nat. Hist.* (12) **2** : 511.
Onychiurus octopunctatus Handschin, 1920, *Ver. naturf. Ges. Basel* **32** : 20.

Bagnall erected *discrepans* mainly on the basis of the differences in pseudocelli between Handschin's species and the true *octopunctatus* of Tullberg. The species must be admitted since *P. octopunctatus* (Tullb.), which has been carefully described by Stach (1954), has also a rudimentary furcula and a ventral organ in the male, both of which are absent from Handschin's specimens. These species are discussed by Stach (1954 : 75) and *discrepans* Bagnall is accepted by him. Bagnall placed *discrepans* in his genus *Dimorphaphorura*, but it is obviously a species of *Protaphorura*. Furthermore, in describing it he states that there are 1 + 1 pseudocelli on Th. I and Th. II, which is incorrect. There are, according to Handschin, 0 + 0 pseudocelli on Th. I and 1 + 1 on Th. II and Th. III.

A slide in the Bagnall collection labelled *O. limnicola* Bag. is undecipherable and, as this name does not appear in the literature, I have made no attempt to place this specimen correctly.

PART III

Two New Species of Onychiurinae

Amongst Bagnall's collection were two slides, both labelled as "Types" and bearing the names *O. millsianus* and *O. differens*. On examination both proved to be new species for which no descriptions have yet been published and I have therefore decided to describe them. *O. millsianus*, under the more correct connotation of *millsi*, falls into the genus *Paronychiurus*, and *differens* into the genus *Handschiniella*, with the specific name changed to *bagnalli*.

Handschiniella bagnalli sp. n. (Figs. 54–57)

Sensory organ on Ant. III with 5 papillae, 5 guard setae, 2 large, strongly bent, smooth sense clubs and a pair of short, straight sense rods (fig. 57). Papillae rather stout and 4 of them more or less parallel-sided. Postantennal organ with 20–22 long foliaceous vesicles, touching and overlapping, much as in *S. thalassophilus* (fig. 64); basal chitinous thickenings of the vesicles clearly visible.

Pseudocelli not very easy to see, small, being not much larger on the antennal base than 3–4 cuticular granules (fig. 54); arranged as follows:

Ant. base: 3 + 3, as in fig. 54.
Hind margin: 2 + 2.
Th. I: 0 + 0.
Th. II, III, Abd. I, II, III, IV: 2 + 2.
Abd. V: 3 + 3, with the inner one on each side larger than the others.
No furcal rudiments visible.

Claw without teeth, but with a moderately long basal seta to each side; unguiculus lanceolate, passing into terminal filament that over-reaches apex of claw (fig. 56).

Two anal spines without papillae, well separated and with associated setae as shown in figure 55. Spines 18, hind claws 13.

Clothing, sparse, of short setae with some longer setae posteriorly. Length up to 0·85 mm.

Scotland: Gleneagles, under stones, 6.i.1934.

Paronychiurus millsi sp. n. (Figs. 78–81)

Sensory organ on Ant. III with 4 rather short stout papillae, 4 guard setae, 2 very large spherical finely granulate sense clubs and a pair of moderately long sense rods (fig. 79). Postantennal organ of 18 compound vesicles, so strongly tuberculated that they appear almost as a double row of closely packed tubercles, and the outlines of the primary vesicles become evident only on careful examination (fig. 78).

Pseudocelli extremely small with, however, a suggestion of a narrow chitinous edging; arranged as follows:

Ant. base: none as such, but 2 close together outside antennal base area, as shown in figure 78.
Hind margin: 0 + 0.
Th. I: 0 + 0.
Th. II, III and Abd. I: 1 + 1 each, very small, not much larger than 1–2 cuticular granules and each surrounded by a bare space and a circle of cuticular granules (*see* fig. 78).
Abds. II and III: 0 + 0.
Abd. IV: 2 + 2, similar to the others but a little larger.
Abd. V: 1 + 1, similar to the others but a little larger.
Antennal base area distinctly marked by smaller cuticular granules,

Anal spines short, curved on large papillae and with 9 long dorsal or dorsolateral and 6 ventral associated setae (*see* fig. 81). Spines 12, papillae 4, hind claw 25.

Claw very stout, without teeth, granulated basally, with an inner basal ridge and a moderately long basal seta on each side. Unguiculus broad, parallel-sided and granulated basally, distally tapering to a fine point that over-reaches apex of claw (fig. 80).

Furcal rudiments absent. Genital pore conical and bearing many short setae.

Clothing, sparse, of short simple setae; larger setae on Abds. V and VI. Cuticle rather coarsely granulate, with smaller granulations along the intersegmental margins.

Length to 1·2 mm.

U.S.A., Iowa: Cedar Rapids, amongst old leaves, 10.xi.1935 (*Andre*).

Summary

This paper comprises the first three parts of a study which is largely devoted to a critical review of Dr. R. S. Bagnall's work on the Collembola Onychiuridae. In Part I the generic and suprageneric classification of both the Tullbergiinae and Onychiurinae is discussed. A new and revised scheme of classification, based on evolutionary considerations, is proposed, and a key for the separation of the subfamilies and genera of the Onychiuridae is included. In Part II Bagnall's species of Onychiurinae are discussed and type specimens of other Onychiurid material in the Collembola collections of the British Museum (Natural History) are reviewed and illustrated. Part III contains the descriptions of two new species. Part IV, which will follow later, will discuss Bagnall's species of Tullbergiinae.